

A BIOSYSTEMATIC STUDY OF THE
POA SECUNDA COMPLEX

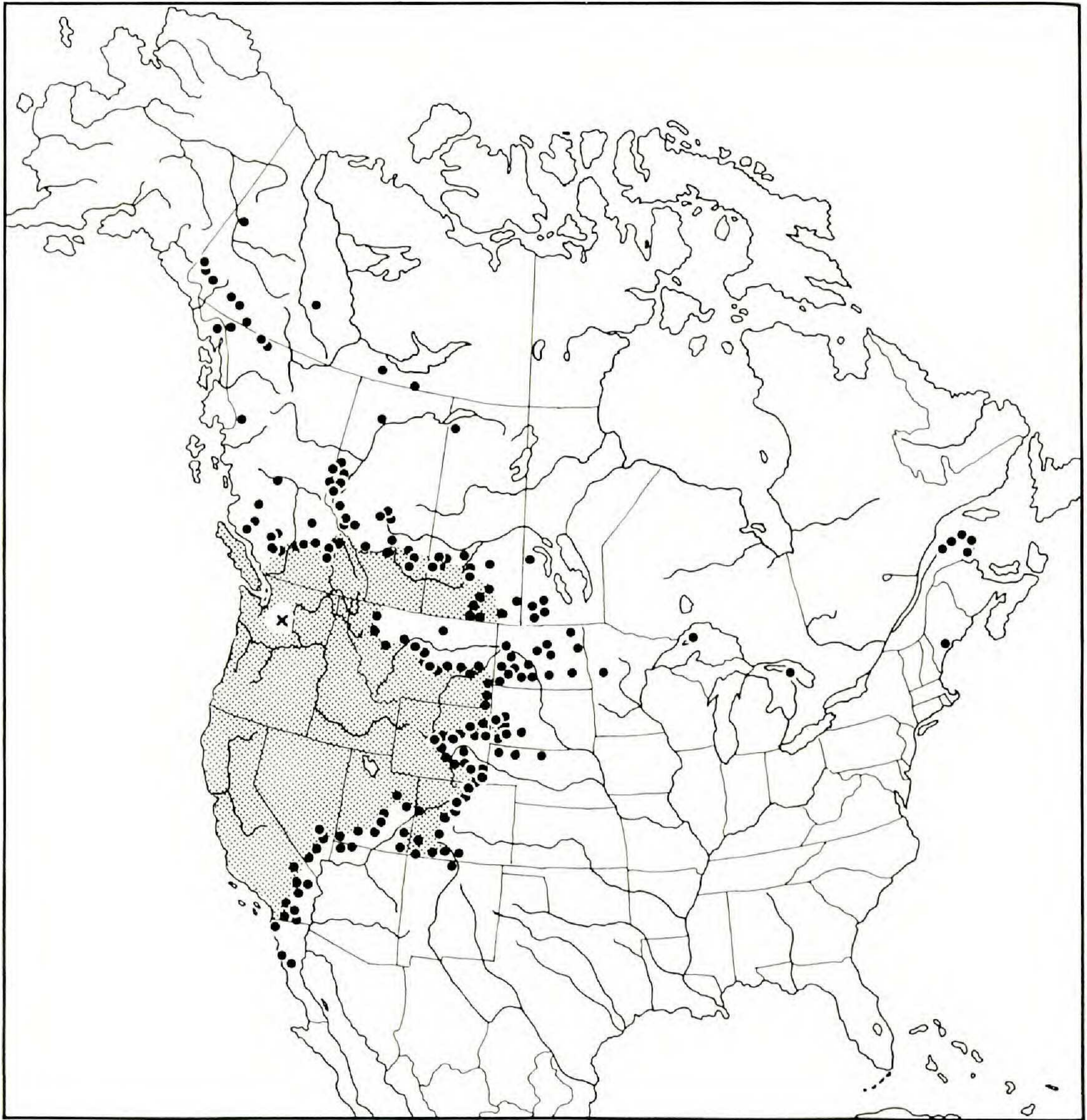
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THE GENUS *Poa* L. comprises taxa with extraordinary ecological diversity and highly varied reproductive biology, yet with equally unusual morphological uniformity. It has a worldwide distribution, occurring mostly in temperate areas in both hemispheres and on all continents except Antarctica. It probably includes more than 200 species, about a quarter of which occur in the Pamirs and Himalayas; other centers of diversity are Alaska, Iceland, and Kamchatka (Hartley, 1961). Habitats range from moist meadows to warm deserts, from sea level to nearly 4000 m, and from the arctic to equatorial regions. Some species are fully sexual, whereas others are partial or obligate apomicts; both inbreeding and fully outbreeding and dioecious species also occur (Clausen, 1961).

Most workers have attempted to divide the genus into subgenera and/or sections, but the resulting classifications have not been similar (Bentham & Hooker, 1883; Hackel, 1887; A. S. Hitchcock, 1950; Marsh, 1952; Edmondson, 1978). Some of these classifications are compared in TABLE 1. In general there are few reliable characters on which to base such classifications; the ones that have been used most often are habit, size and pubescence of various plant parts, and sex of flowers. Habit is a reflection of mode of branching (extra- or intravaginal), and this character can also be used to delimit large groups of species. However, size and pubescence characters are quite unreliable in some groups, often varying widely with environment or even within a single plant. Mode of apomictic embryo-sac formation, whether aposporous or diplosporous, may be useful for creating a subgeneric classification; however, this character has not been studied for most species and would in any case only be applicable to those that are apomictic. There seem to be fertility barriers among some groups of species (see Hiesey & Nobs, 1982).

The *Poa secunda* Presl complex (also known as the *P. sandbergii* Vasey complex; see next section) is a widespread, difficult group; it is distributed over most of western North America, with disjunct populations in the Gaspé Peninsula of Quebec and others in Chile (MAP 1). The plants occur in a wide range of habitats, from low deserts to high alpine areas in the Sierra Nevada and the Rocky Mountains; most grow in relatively dry sites, but some occur in wet meadows or in damp gorges. There are currently 45 epithets in the group, and these have historically been included in from one to 11 species.

The results of Heidel and colleagues (1982) and Gilmartin and coworkers (unpubl. MS) illustrate the nature of the taxonomic problem. Both groups



MAP 1. Distribution of *Poa secunda* complex in North America. Cross shows distribution of *P. curtifolia*. Within shaded area collections too numerous to show individually.

looked at sets of vegetative and floral characters, comparing variation within and between several populations of *Poa secunda* in eastern Washington. They found that for the vegetative characters the ratio of inter- to intra-population variance was similar to that of other unrelated grass species; for the floral characters, however, variance within populations was unusually low compared to that between populations. With respect to floral characters, in other words, populations of *Poa secunda* are more differentiated than those of other grasses, although my own data show that this differentiation never leads to complete discontinuity. Faced with this low but perceptible differentiation, some taxonomists have recognized the "units" taxonomically.

The complex is commonly distinguished from the rest of the genus by the lack of a prominent keel on the lemma. I have examined lemma cross sections of 15 different species of *Poa* to determine the anatomical basis of this character,

TABLE 1. A comparison of five classifications of the genus *Poa*.*

HACKEL (1887)	BENTHAM AND HOOKER (1883)	EDMONDSON (1978)	HITCHCOCK (1950)	MARSH (1952)
Subg. <i>Dioicopoa</i>	Subg. <i>Dioicopoa</i>	Subg. <i>Dioicopoa</i>		Subg. <i>Dioecia</i> Subg. <i>Pistillata</i>
Subg. <i>Eupoa</i>	Subg. <i>Eupoa</i>	Subg. <i>Poa</i> Sect. <i>Ochlopoa</i> Sect. <i>Coenopoa</i> Sect. <i>Stenopoa</i> Sect. <i>Bolbophorum</i> Sect. <i>Poa</i> Sect. <i>Tichopoa</i> Sect. <i>Homalopoa</i> Sect. <i>Cenisia</i> Sect. <i>Macropoa</i> Sect. <i>Leptophyllae</i> Sect. <i>Oreinos</i> Sect. <i>Abbreviatae</i> Sect. <i>Nanopoa</i>	Sect. <i>Annuae</i> Sect. <i>Palustres</i> Sect. <i>Alpinae</i> Sect. <i>Pratenses</i> Sect. <i>Homalopoeae</i> Sect. <i>Epiles</i> Sect. <i>Scabrellae</i> Sect. <i>Nevadenses</i>	Subg. <i>Secundae</i>
Subg. <i>Poidium</i> Subg. <i>Pseudopoa</i>	Subg. <i>Poidium</i> Subg. <i>Pseudopoa</i> Subg. <i>Leucopoa</i>			

*The first two classifications include the entire genus, the third only attempts to classify the European species, and the fourth and fifth include only North American species. Corresponding sections in Edmondson's and Hitchcock's classifications overlap only in part.

and I have found no appreciable difference in cross section between the *P. secunda* complex and other members of the genus. All species examined have two or three layers of sclerenchyma on the abaxial side of the middle vascular bundle, and these layers taper evenly to a single layer on both sides of the vein. Because the keel has no anatomical basis, and because specimens cannot easily be determined as keeled or nonkeeled, it may be an unreliable taxonomic character.

More consistently useful distinguishing characters are the lengths of the rachilla internodes (0.6–1.9 mm, vs. < 0.5 mm for most other members of the genus) and the spikelets. Anthers are long (1–4.2 mm), whereas those of many other bluegrasses are less than 1 mm. The plants are perennial and caespitose, with intravaginal branching; the panicles are mostly narrow, and the flowers are perfect, although frequently pollen sterile. Although there is often a tuft of hairs on the callus, the long, tangled, cobwebby hairs characteristic of many other species of *Poa* are lacking.

Spikelet shape and rachilla-internode length are the most distinctive characters of the *Poa secunda* group in comparison to the rest of the genus; most other bluegrasses have more or less ovoid spikelets with a very short internode between the first two florets. Intravaginal branching distinguishes all the caespitose bluegrasses from A. S. Hitchcock's sections *Homalopoeae*, *Palustres*, and *Pratenses*. The lack of a prominent cobweb at the base of the lemma also distinguishes the *P. secunda* group from most members of the latter two sections. The perennial habit distinguishes it from section *Annuae*, which is made up entirely of annuals.

The *Poa secunda* complex is defined more by exclusion than by inclusion; there is thus no evidence that the group is strictly monophyletic (i.e., including only and all the descendants of a single ancestor). The long rachilla internodes and elongate spikelets might be considered apomorphies (unique, derived features) characterizing the group, but then such imperfect-flowered species as *P. cusickii* Vasey and *P. epilis* Scribner would have to be included as well. These latter two species may, in fact, prove to be obligately apomictic descendants of *P. secunda*, but this is only speculation at the moment. The whole notion of apomorphy, however, is difficult to apply in a genus in which there is probable hybridization. In such a group cladistic analysis is not appropriate, since it is based entirely on an assumption of branching evolution (but see Fink, 1982, for discussion of cladistic treatment of hybrids).

Sister groups might be sought in Hitchcock's (1950) sects. *Alpinae* or *Epiles*, as was suggested by Clausen and Hiesey (1958). The taxa in these sections are, like *Poa secunda*, mostly caespitose; they are alpine or arctic in distribution. They all lack a cobweb on the lemma. Such evidence does not allow inference of phylogeny but at least permits elimination of some possible sister groups. Because there are fertility barriers and differences in branching, embryo-sac formation, and spikelet size and shape, *P. secunda* is probably not closely allied to *P. nemoralis* L., *P. sylvestris* Gray, *P. autumnalis* Muhl., or *P. palustris* L. or other members of sect. *Palustres* (Kellogg, 1983; see also Hiesey & Nobs, 1982).

This study had three major goals: to analyze the pattern of morphological variation in the *Poa secunda* complex (and to assess the level at which taxonomic characters varied, whether within the individual, within a population,

or between populations); to decide how many taxa the complex represented; and to investigate the reproductive biology of the group and its role in producing the pattern of morphological variation.

HISTORY OF SYSTEMATIC TREATMENTS

The type specimen of *Poa secunda* was collected by Thaddeus Haenke "in cordilleris Chilensibus" probably sometime between 1790 and 1794 and was described by Presl in *Reliquiae Haenkeanae* in 1830, making this the oldest valid name in the group. Later in the century, collectors in the western United States, particularly Vasey, Piper, Scribner, and Rydberg, found and described many of the other species included in the *P. secunda* complex, beginning with Sandberg's collection near Lewiston, Idaho, in 1892 of the plant that bears his name. Names proliferated, often without much justification. A case in point is Scribner's (1883, p. 66) description of *P. nevadensis*, in which he stated "The characters of the grass agree in many points with those of *Atropis scabrella*, Thurber, in Bot. Calif. ii, p. 310, but whether it be the same I am unable to say, having never seen any authentic specimens of that species." He then went on to publish the name *Poa nevadensis* as a new species.

By 1935 more than 40 names had been published. Jones (1912) had proposed an extensive synonymy, but it had not been accepted. In 1935 A. S. Hitchcock finally resolved some of the chaos by dividing the group into two sections, *Scabrellae* and *Nevadenses*, each with four species. Most other works since Hitchcock's *Manual of the Grasses of the United States* have followed his classification, recognizing similar—if not identical—groups of species.

Hitchcock's (1935) keys and descriptions were soon seen to be a poor reflection of the variation observed in nature. C. L. Hitchcock and colleagues (1969) stated that the range of variation in the complex is so continuous that were the populations freely interbreeding, the group should be regarded as a single polymorphic taxon. Cronquist and co-workers (1977) concluded that the distinction between sects. *Scabrellae* and *Nevadenses* is quite artificial—useful for keying purposes but tending to belie the close relationship among all the species. Marsh (1952) simply synonymized all the members of the group, recognizing only the single species *Poa secunda*; his treatment, however, has not been followed.

Authors have also disagreed on the relationship between the South American *Poa secunda* and the North American *P. sandbergii*; for a detailed review of the literature on the question, see Arnow (1981). Arnow compared North and South American populations both morphologically and ecologically, concluding that there is no reason to separate them and therefore that *P. secunda* is the appropriate name for the species. My observations support her conclusion.

METHODS

As noted below, taxa in *Poa* are recognized primarily on the bases of the size of parts and the presence or absence of trichomes and scabrosities on various parts of the plant. The core of any taxonomic revision within the genus must therefore involve a detailed analysis of variation in these characters.

PLANTS AND CHARACTERS: PRODUCTION OF THE DATA MATRIX

The analysis of character variation was done on two separate sets of plants. The first set consisted of 95 plants chosen to represent the full range of geographic and morphological variation (see APPENDIX 1). At least one plant was chosen from each of the states or provinces in which the species occurs, with additional plants taken from some states to include the extremes of morphological variation. The second set was chosen to evaluate variation within populations ("population" is defined here as plants growing in close proximity to each other, with no implication about the extent of interbreeding). Such an evaluation was necessarily limited by the collections available. Most of these populations were my own collections and included groups of plants that had been growing within a few meters of each other. For some of the "populations," however, I had to use herbarium collections with the same or sequential collection numbers from the same locality. All plants are listed in APPENDIX 2. Each of the populations could be placed in one of four broad morphological groups: large plants with short ligules, those with open panicles, those characteristic of *Poa curtifolia*, and "ordinary" *P. secunda*.

Plants were scored for the following 60 characters:

Nonvarying or nearly so

1. habit of plant
2. scabrousness of ligules
3. decurrence of ligules
4. ciliate nature of ligule margins
5. scabrousness of leaf margins
6. scabrousness of panicle branches
7. scabrousness of rachis
8. scabrousness of glume keels
9. ciliate nature of glume margins
10. shape of glume apexes
11. shape of lemma apexes
12. ciliate nature of lemma margins
13. no. of lemma nerves

Environmentally controlled

14. color of culms
15. involution of leaves
16. glaucousness of leaves

Varying as much within a clone as within the complex

17. no. of nerves in 1st glumes
18. no. of nerves in 2nd glumes
19. scabrousness of glumes next to keel
20. scabrousness of leaf midveins

Varying as much within a population as within the complex

21. scabrousness of culms
22. width of culms
23. scabrousness of sheaths
24. scabrousness of abaxial side of leaves
25. scabrousness of adaxial side of leaves
26. no. of branches at 1st panicle nodes
27. no. of branches at 2nd panicle nodes
28. no. of branches at 3rd panicle nodes
29. pubescence of rachillas
30. tuft of hairs on calluses
31. scabrousness of lemmas
32. length of pubescence on 1st lemmas
33. distribution of pubescence on lemmas
34. length of hairs on lemmas
35. length of pubescence on 1st paleas
36. hairs or teeth on palea keels
37. pubescence of paleas
38. shape of lodicules

Ranges of variation overlapping among populations

39. height of plant
40. height of flag leaves
41. length of flag leaves
42. length of basal leaves

- | | |
|--|--------------------------|
| 43. shape of panicles | 52. length of spikelets |
| 44. length of panicles | 53. length of 1st glumes |
| 45. distance from 1st to 2nd panicle nodes | 54. length of 2nd glumes |
| 46. distance from 2nd to 3rd panicle nodes | 55. width of 1st glumes |
| 47. width of leaves | 56. width of 2nd glumes |
| 48. shape of ligules | 57. length of lemmas |
| 49. length of ligules | 58. length of paleas |
| 50. no. of florets per spikelet | 59. length of anthers |
| 51. length of 1st rachilla internodes | 60. length of lodicules |

This list includes all characters used in earlier keys, as well as many others suggested by close inspection of the specimens. For all quantitative characters five measurements were taken from each specimen and averaged. The mean was used in the final data matrices unless only integral values were possible (e.g., number of branches per panicle node), in which case the mode was used.

After scoring and recording character values for each plant, I could remove from the analysis those characters that were invariant, those that varied as much within as between individuals, those that varied as much within as between populations, and those that were clearly under environmental control (character weighting; see also Davis, 1983).

For assessment of variation among the offspring of self-pollinated plants, seeds from plants that I had self-pollinated in 1981 were stratified and planted in the greenhouse in early autumn. Percentage of germination was comparatively low in all cases, but two plants (*Kellogg 29*, from Nez Perce Co., Idaho, and *Kellogg 122* from Morrow Co., Oregon, both corresponding to *Poa canbyi*) produced a large number of surviving offspring; I will refer to these as families 29 and 122, respectively. Fourteen plants in family 29 and 17 in family 122 bloomed in the spring of 1983. The plants of each family were measured for height of plant, length of panicles, length of basal leaves, height and length of flag leaves, width of leaves, length of ligules, distances from the first to the second and from the second to the third panicle nodes, number of florets per spikelet, length of spikelets, length of first and second glumes, length of lemmas, paleas, and anthers, length of first-rachilla internodes, and extent of lemma pubescence (all from the fifth section of the character list).

NUMERICAL TAXONOMY: ANALYSIS OF THE DATA MATRIX

The analysis of the data matrix in taxonomy is simply a search for pattern, where pattern is defined as sets of correlated characters (see, for example, Sneath & Sokal, 1973). This correlation is not linear, however, but rather what Farris (1969) has called hierarchical. Because Farris's term uses neither the word hierarchical nor the word correlation in the usual sense, I will refer to such characters as concordant—i.e., producing a taxonomically useful pattern. Groups of concordant characters allow us to recognize groups of organisms; in such groups of characters, certain combinations of values do not occur, leaving "gaps" in the distribution of points. The distinction between concordant and

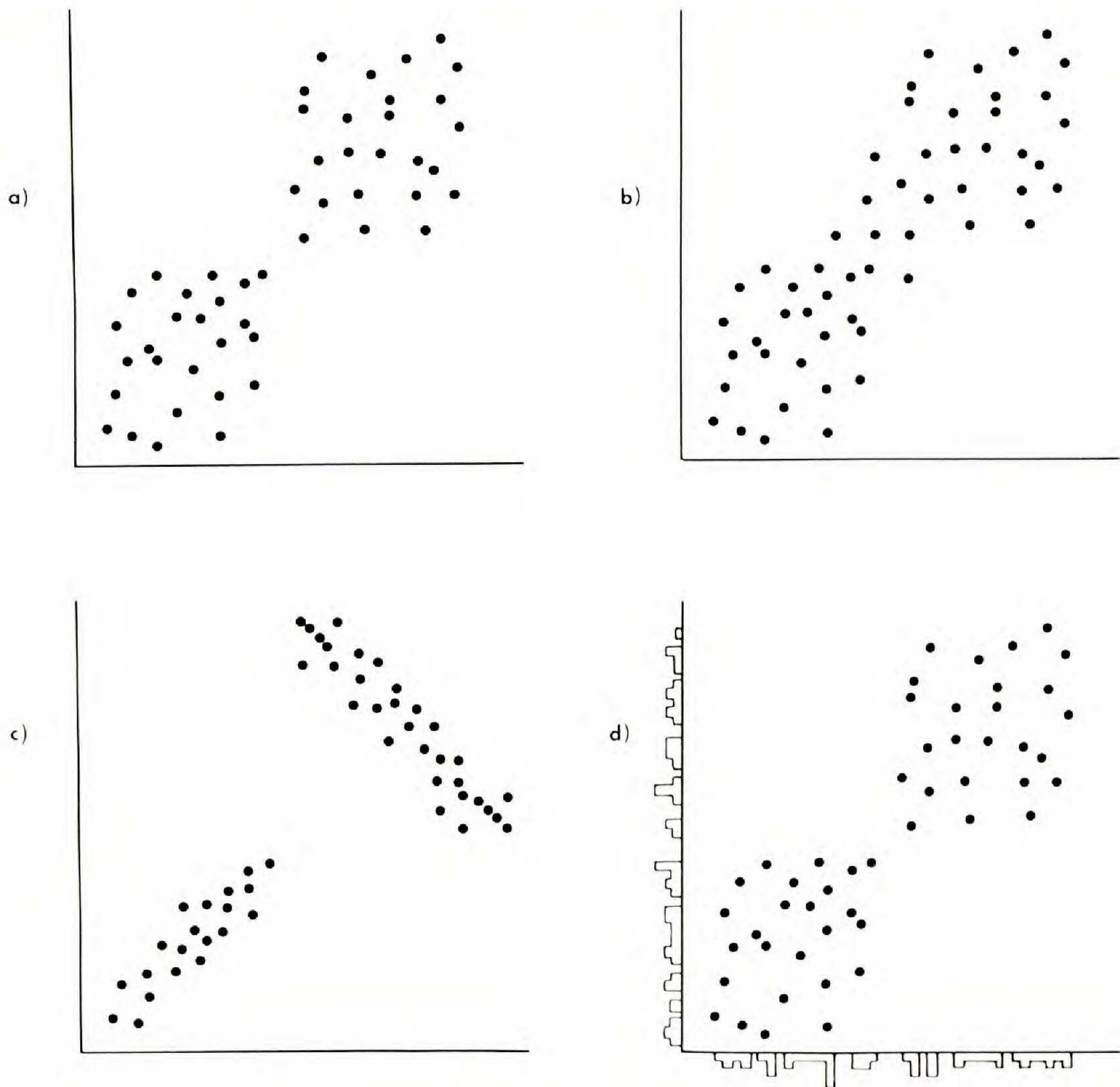


FIGURE 1. Distinction between correlated and concordant characters: a, characters linearly correlated ($r = 0.83$) and concordant; b, characters linearly correlated but not concordant ($r = 0.82$); c, characters less well correlated but concordant ($r = 0.65$); d, same data set as a, but with histograms for each character displayed on axes, characters almost continuously distributed but still concordant. Axes = values of a continuously varying morphological character, points = organisms.

linearly correlated characters is shown by comparison of FIGURE 1a–d. In FIGURE 1a the overall linear correlation coefficient (r) is 0.83; here the two characters are both linearly correlated and concordant in that they define two nonoverlapping sets of organisms. FIGURE 1b, on the other hand, shows two characters that have a similar linear correlation ($r = 0.82$) but no possibility of hierarchy since the characters do not define discrete sets of points. Finally, in FIGURE 1c, the characters are concordant but linear correlation is reduced ($r = 0.65$). FIGURE 1d shows histograms projected onto the axes of the same graph as 1a, showing that the univariate distribution of points is not dramatically bimodal; clearly, though, the lack of points in the lower right and upper left corners creates both the high correlation coefficient and the gaps that allow us to partition the points into two groups.

I began my search for pattern by using univariate, bivariate, and multivariate statistical techniques to examine various combinations of characters; I looked for concordance among the characters and for nonoverlapping sets of organisms.

Multivariate techniques have been applied to many groups of grasses in the past (Morishima & Oka, 1960; Goodman, 1968; Phipps, 1970; Clayton, 1971; Baum, 1974; Barkworth, 1978; Williamson & Killick, 1978; Doebley & Iltis, 1980). I chose to begin with principal-component analysis, a multivariate method that considers each plant as a point in multidimensional space, where each dimension is a taxonomic character. It is possible to visualize the relative positions of the plants on axes that are combinations of characters by mathematically reducing the dimensionality of the hyperspace. Plotting of the OTUs (operational taxonomic units—individual plants in this case) against pairwise combinations of the factors may make discontinuities between the clusters detectable (see, for example, McNeill, 1975). Each axis (factor) is a linear combination of several taxonomic characters; these characters are said to be “loaded” on that axis. By examining the factor loadings, one can determine which characters are responsible for explaining most of the variance in the data matrix. I performed a variety of principal-component analyses on different sets of plants and characters (see TABLE 2).

There are three major problems with the use of principal-component analysis. First, because it assumes multivariate normality, binary or multistate characters may be weighted disproportionately by the algorithm. I therefore ran one analysis with only the quantitative characters. Second, this type of analysis is strongly affected by outliers. I therefore did another analysis excluding all the representatives of *Poa curtifolia*. Third, principal-component analysis will pick out only the most distinct groups in a set of OTUs, partly because it is designed to find linear correlations among characters that, as shown earlier, may or may not be taxonomically concordant. The results thus have one-sided implications: if a group is found to be discrete, then it probably really is quite distinct, but the converse does not hold.

Discriminant analysis is useful for comparison with principal-component analysis in that it allows one to compare variation within populations to overall variation in the data matrix. Although discriminant analysis could be used to test the validity of previously described taxa, there is an element of circularity in using it in this way. Because such analyses attempt to minimize variance within groups relative to that between them, they effectively assume that the groups to which the OTUs are assigned are somehow real entities. Furthermore, by assigning plants to groups *a priori*, the taxonomist can only test whether those particular groups are nonrandom—very different from testing whether they in fact represent sets of concordant characters. If there are discrete groups in the complex that are quite different from the ones being tested, they may easily go undetected in a discriminant analysis. To minimize prejudice in the analysis, I therefore used populations as the groups. Cluster analysis is also commonly utilized in studies of this sort, but because this imposes a hierarchical structure on the data (Gower, 1967), it would be circular to use it to test for

the presence of such structure (and inappropriate to use it in a hybridizing group).

Because of the difficulty of obtaining adequate population samples, I had to restrict the discriminant analyses to two populations of *Poa curtifolia*, five populations of large plants with short ligules, and three populations of open-panicled plants, with the rest being plants from southern California and the Gaspé Peninsula. Such a sample is clearly highly biased toward recognizing discrete groups; it thus has one-sided implications opposite those of principal-component analysis. Nondiscrimination of groups convincingly shows their morphological indistinctness, but discrimination does not prove that groups are discrete.

RESULTS

CHARACTERS STUDIED

All members of the complex have a caespitose habit (1).¹ The only exception is *Poa curtifolia*, which sometimes produces short rhizomes, although it maintains the intravaginal branching characteristic of the rest of the group.

Many plants, particularly those on dry sites, become red with age (14). As Arnow (pers. comm.) has also observed, this character varies within a site. Plants that are red in their native habitat are often green when grown the next season in the garden, and all plants are green when grown in the greenhouse. This character is thus environmentally controlled. Members of the complex are frequently glaucous (16), with a waxy coating on the leaves, but this also depends on the environment in which the plants are grown. The one exception to this is *Poa curtifolia*, which is glaucous in any environment, although the extent to which the culms become red varies among individual plants. In general, larger plants are more likely to be strikingly glaucous, whereas smaller ones are more likely to become red during development. Because these characters are not consistently expressed, however, they cannot be used as reliable taxonomic characters, except to distinguish *P. curtifolia*. Such characters can be used to reinforce an existing classification but not to establish it.

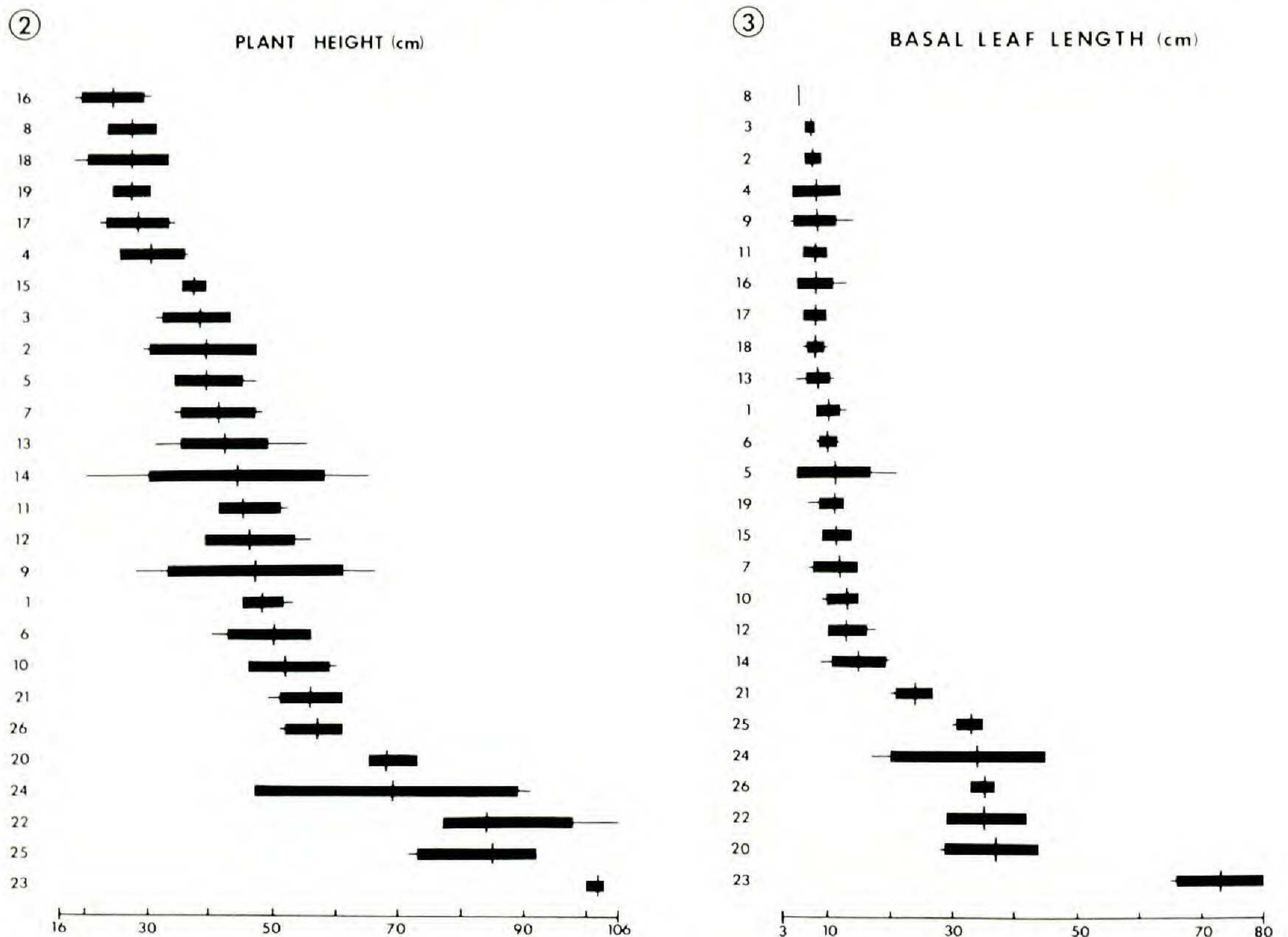
Height of plants (39) (greater vs. less than 3 dm) has been used as a specific character in previous classifications. This character varies considerably with environment, among members of a population, and within a clone. Some relative differences in size persist in the garden, so this character may still help distinguish groups within the complex. The range of variation is great within populations, however, and there is considerable overlap between them (FIGURE 2).

All members of the complex have a conspicuous tuft of more or less erect basal leaves; these sometimes become more lax when the plants occur on very wet sites (such as the open-panicled plants growing near Multnomah Falls, Oregon, in wet canyons). The length of the basal leaves (42) varies within and among populations (see FIGURE 3). The flag leaf (the uppermost leaf on the

¹Numbers in parentheses refer to character numbers in the list of characters.

TABLE 2. Summary of multivariate analyses.

ANALYSIS	PLANTS INCLUDED	CHARACTERS USED	ILLUS- TRATION (figure no.)	CUMULATIVE PERCENT OF VARIANCE			CANONICAL CORRELATIONS			AXES WITH EIGEN- VALUES > 1
				A1	A2	A3	A1	A2	A3	
Principal- component	All in Appendix 1	15, 22, 23, 32, 40, 42, 43, 47, 48	—	39	44	68				3
	All in Appendix 1 except <i>Poa curtifolia</i>	15, 22, 23, 32, 40, 42, 43, 47, 48	16	38	56	69				3
	All in Appendix 1	1-60	17, 18	17	29	38				16
	All in Appendix 1	2-8, 16, 19, 21-37, 39-60	—	20	32	43				13
	All in Appendix 1	17, 18, 26-28, 32, 34, 35, 39-42, 44-47, 49-60	—	28	48	56				7
	All in Appendix 1 except <i>Poa curtifolia</i>	1-60	19	24	36	44				11
Discriminant	All in Appendix 2	23, 32, 39-44, 47-50, 52-54, 57, 59	20	58	71	81	.98	.95	.95	7
	All in Appendix 2 except population 23	23, 32, 39-44, 47-50, 52-54, 57, 59	21	52	66	79	.98	.95	.95	7
	All in Appendix 2	23, 32, 39-41, 43, 44, 47-50, 52-54, 57, 59	—	48	64	77	.98	.95	.94	7
	All in Appendix 2 except population 23	23, 32, 39-41, 43, 44, 47-50, 52-54, 57, 59	—	45	62	77	.97	.94	.94	6



FIGURES 2, 3. Range of variation compared within and among populations: 2, plant height; 3, basal-leaf length. Each bar = separate population. Only 1 population of *Poa curtifolia* (26) shown. Numbers refer to population numbers as listed in APPENDIX 2. Narrow horizontal line = range of values for that population, broad horizontal bar extends 1 standard deviation on both sides of mean, narrow vertical line = mean. Horizontal scale = full range of variation in complex.

culm) is rarely borne much above midpoint on the culm (40) and varies considerably in length (41). The margins of the leaves are scabrous (5). The midvein is frequently scabrous (20) as well, particularly near the tip on the abaxial side of the leaf, but this character varies within an individual, some leaves being scabrous and others not. On some plants leaves are scabrous on either the abaxial (24) or the adaxial (25) side or both, but I have never found a population that was not polymorphic for this character.

Leaf width varies from 0.4 to 4 mm (47; FIGURE 4). Although some basal leaves tend to be somewhat wider than culm leaves, the difference is neither consistent nor, when present, significant. I therefore did not separate leaf width into basal and culm leaf components.

Among herbarium specimens there is considerable variation as to whether the leaves are rolled or flat (15), and this has been widely used as a specific character to distinguish *Poa juncifolia* Scribner from *P. ampla* Merr., and *P. sandbergii* from *P. incurva* Scribner & Williams. However, all plants, if given enough water, have flat leaves. Furthermore, few plants can be found with truly involute leaves. If the leaves are 1.5 mm or less in width, they will tend to appear involute on drying but are actually merely folded.

The ligule of all members of the complex is nonciliate (4), decurrent (3), and more or less scabrous (2), but almost never glabrous. Variation in length (49; FIGURE 5) and shape (48) is almost continuous from short (0.5 mm) and truncate to long (6 mm) and acuminate. Plants with scabrous sheaths (23) are not found in pure populations; they are always mixed with glabrous-sheathed plants. This character has been used in the past to distinguish *Poa scabrella* (Thurber) Benth from the rest of the complex, but the pattern of variation suggests that it is simply a population-level polymorphism.

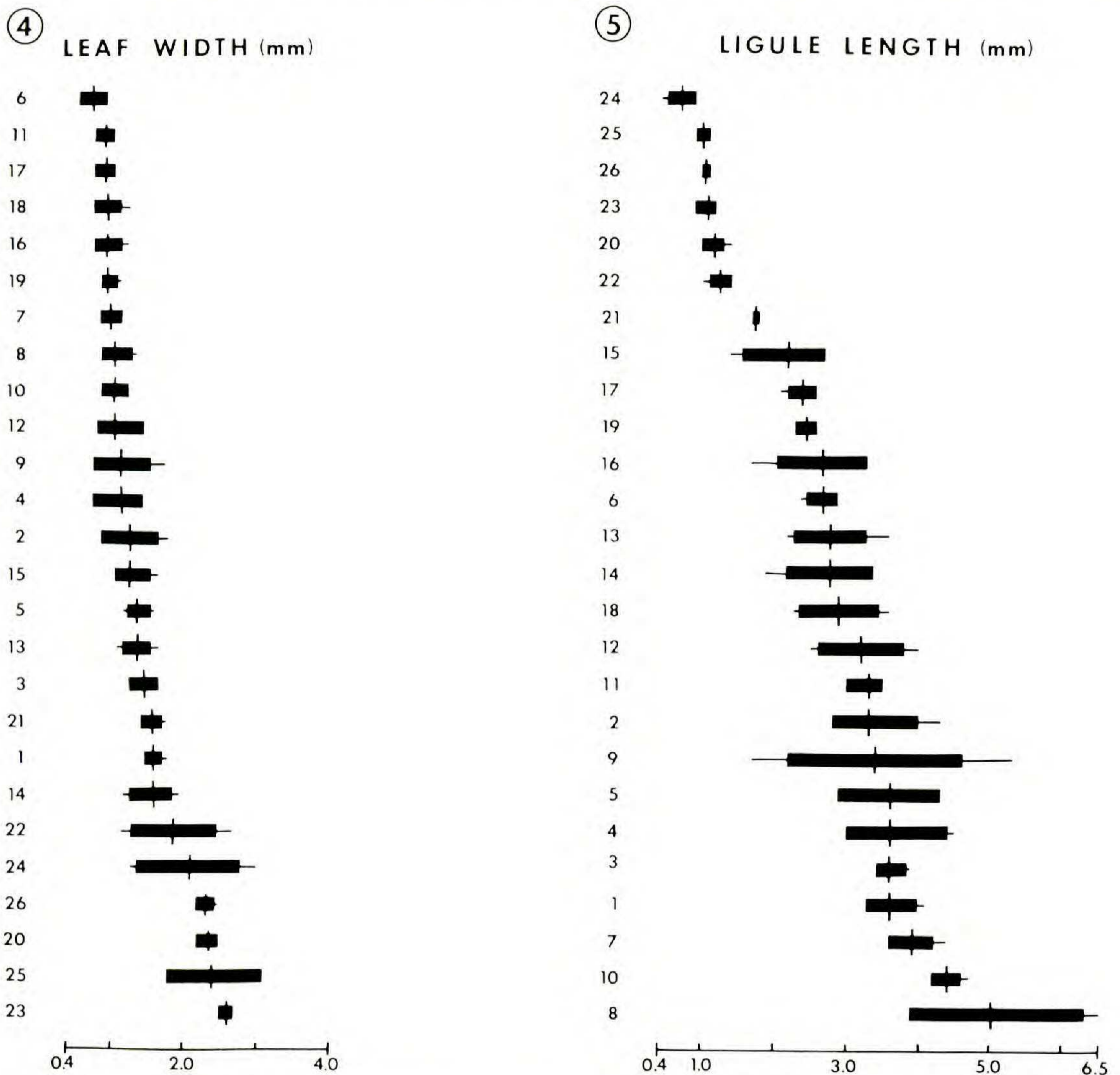
Inflorescences are either contracted or open panicles (43); plants with open panicles are usually referred to *Poa gracillima* Vasey. However, panicles of all plants become open for about a week at anthesis, contracting again afterward in most. Those plants with persistently open panicles occur mainly in montane habitats in the Rocky and Cascade mountains and the Sierra Nevada, and a few are known from Chile (Arnold, 1981). They frequently grow in cracks in granite outcrops but are not restricted to such sites. The open panicle of these plants persists in the garden.

The panicle branches and rachis are scabrous (6, 7) on nearly all specimens. There is considerable variation in culm width (22) just below the inflorescence, in distance between the first and second (45) and the second and third panicle nodes (46), and in number of branches at each of the first three nodes (26–28). Panicle length (44) also varies widely within populations, and the ranges of variation overlap (FIGURE 6).

Spikelets have from two (rarely one) to eight florets (50) and vary greatly in length (52; FIGURE 7). As noted above, the first rachilla internode (51) is relatively long for *Poa* species, varying from 0.6 to 1.9 mm, but variation is continuous among populations. The rachilla may be pubescent, scabrous, or glabrous (29), but this too varies within populations.

Glume and lemma apices are similar in shape (10, 11), mostly acute to nearly obtuse; there is no striking variation within the complex. The upper parts of the margins of both glumes and lemmas are finely ciliate (9, 12), and glume keels are consistently scabrous, at least toward the apex (8). The glumes of most plants each have three nerves (17, 18), although within a clone occasional glumes with one or five nerves can be found. Lemmas are consistently 5-nerved (13). Some glumes within a clone may also be scabrous next to the keel (19), but this character is rarely consistent within a population. Glume width (55, 56) varies almost as much within populations as within the entire complex, and the range of variation in length of the first (53; FIGURE 8) and second (54) glumes overlaps considerably among populations.

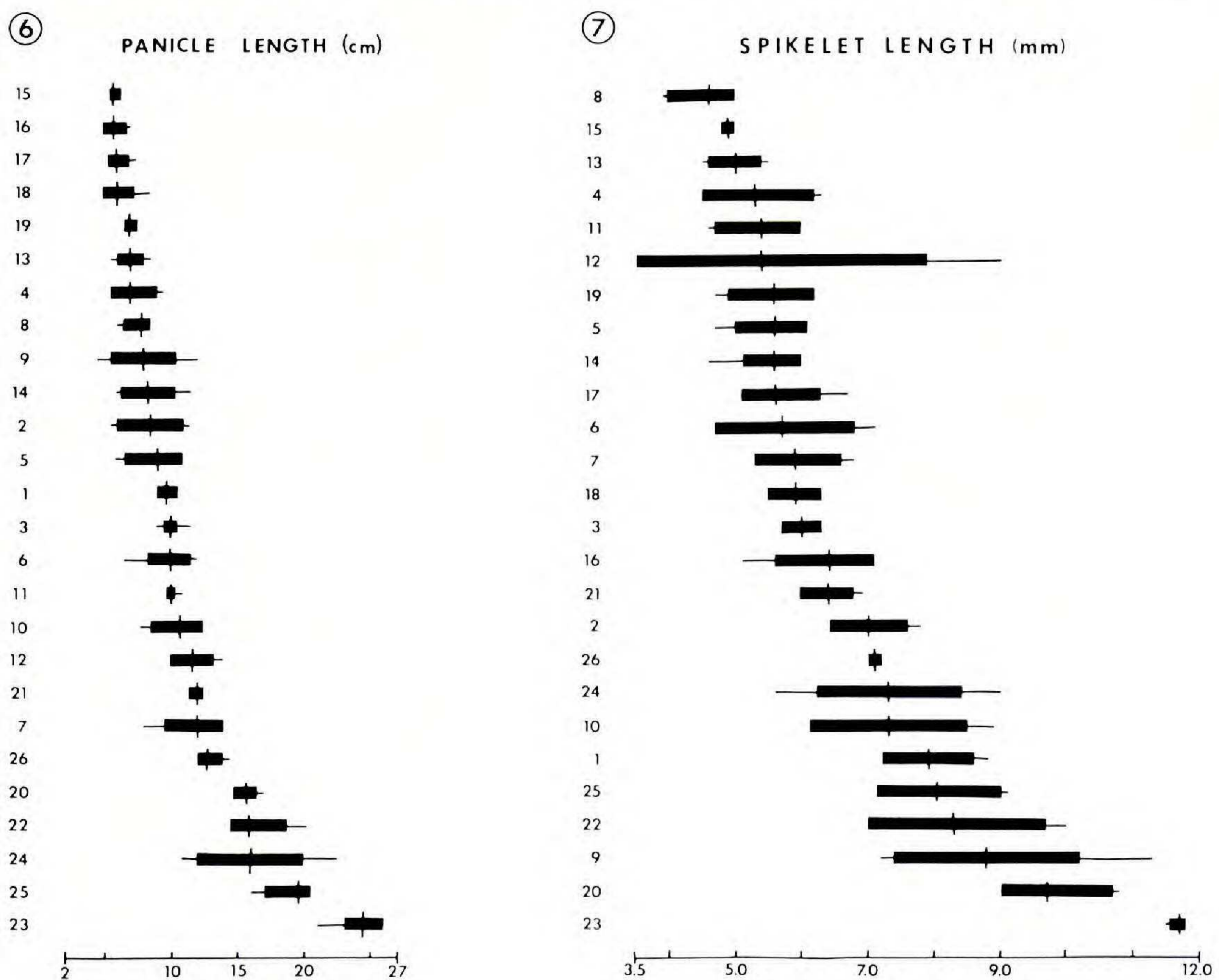
Lemma pubescence (32) is a major character in all classifications of *Poa* and has been heavily relied on in the *P. secunda* complex. *Poa ampla*, *P. juncifolia*, *P. nevadensis*, and *P. curtifolia* have been distinguished from other members of the complex on the basis of their scabrous to glabrous lemmas, and A. S. Hitchcock (1950) put them in a separate section, *Nevadenses*, on this basis. I have found, however, that this character commonly varies within populations, in some cases nearly as much as in the complex as a whole (FIGURE 9). Pubescence can extend up to nearly three-quarters the length of the lemma, but



FIGURES 4, 5. Ranges of variation compared within and among populations: 4, leaf width; 5, ligule length. Format same as in FIGURES 2, 3.

the character varies continuously. In this group lemma pubescence is thus of doubtful taxonomic utility. The lemma may or may not be scabrous above the area where there is pubescence (31); there may also be a small tuft of hairs on the callus (30). The pubescence may be distributed evenly, it may extend somewhat higher on the marginal nerves and keel (33), or it may rarely be confined only to the keel and margins, not occurring between; the trichomes may be as much as 0.3 mm long (34). All these characters vary at the population level. Lemma length (57) is relatively less variable within populations, but the ranges of variation overlap between populations (FIGURE 10).

Palea pubescence (37) has been useful in separating other species of *Poa* (e.g., *P. reflexa* Vasey & Scribner and *P. leptocoma* Trin.; Soreng & Hatch, 1983), but it is too variable to be of help in *P. secunda*. Paleas may be pubescent, scabrous, or glabrous, but all character states occur in almost every population studied. The palea keels may have either hairs or teeth (36), but this too varies



FIGURES 6, 7. Ranges of variation compared within and among populations: 6, panicle length; 7, spikelet length. Format same as in FIGURES 2, 3.

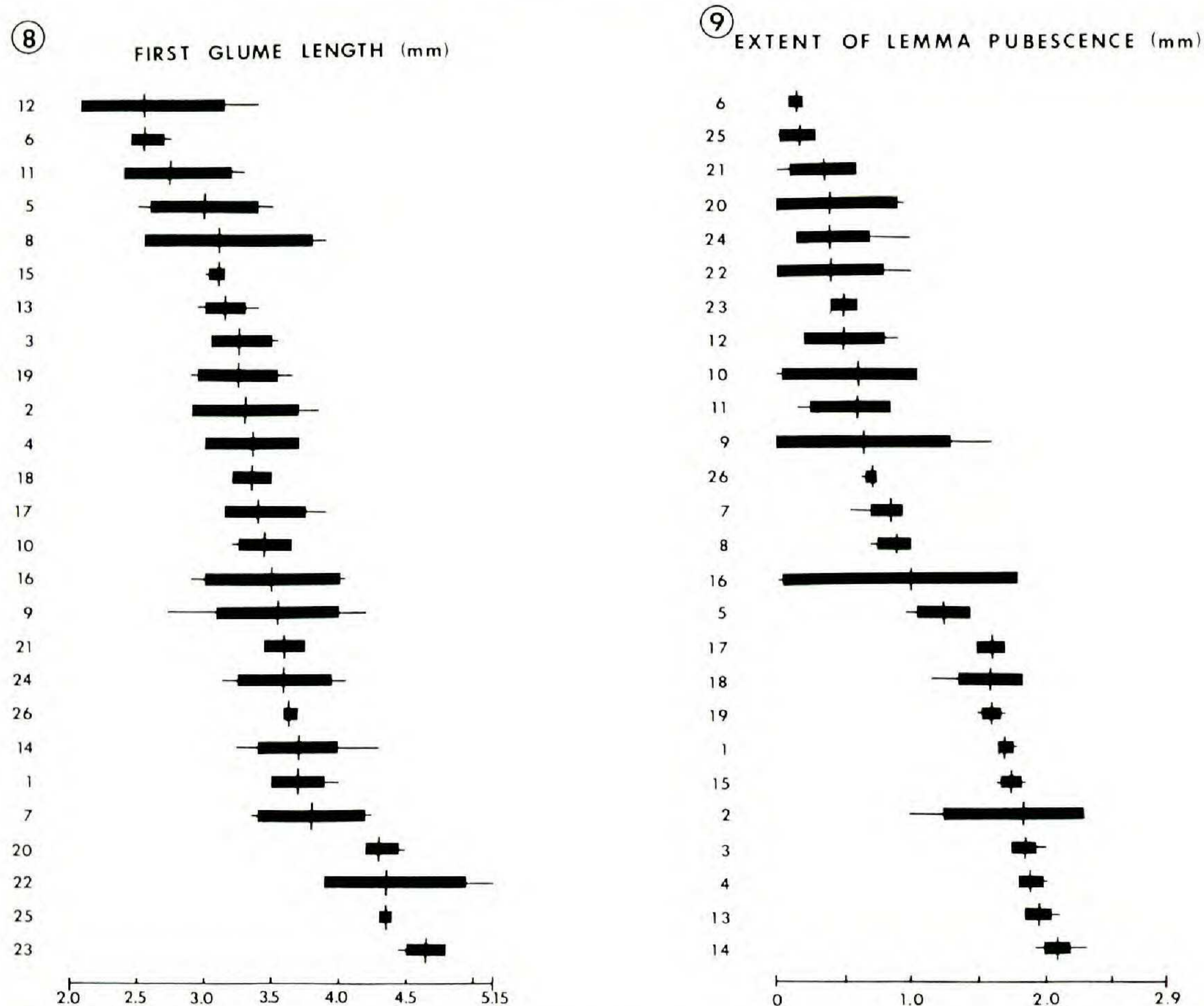
within populations. The length of the hairs (35) is variable: long hairs near the bottom of the palea nerves frequently grade into stiff teeth nearer the top. Again, the only remaining character is palea length (58), which shows considerable overlap among populations.

Lodicule shape (38), like lodicule length (60), varies as much within as between populations. Anther length (59) also varies within and between populations (FIGURE 11).

VARIATION AMONG OFFSPRING OF SELF-POLLINATED PLANTS

The offspring of plants I self-pollinated showed substantial variation within each family. I gave a set of the offspring and a traditional key (C. L. Hitchcock & Cronquist, 1973) to taxonomists not familiar with the group; they identified the offspring of each family as a mixture of *Poa scabrella*, *P. nevadensis*, and *P. gracillima*. Individual plants were generally identified differently by different taxonomists.

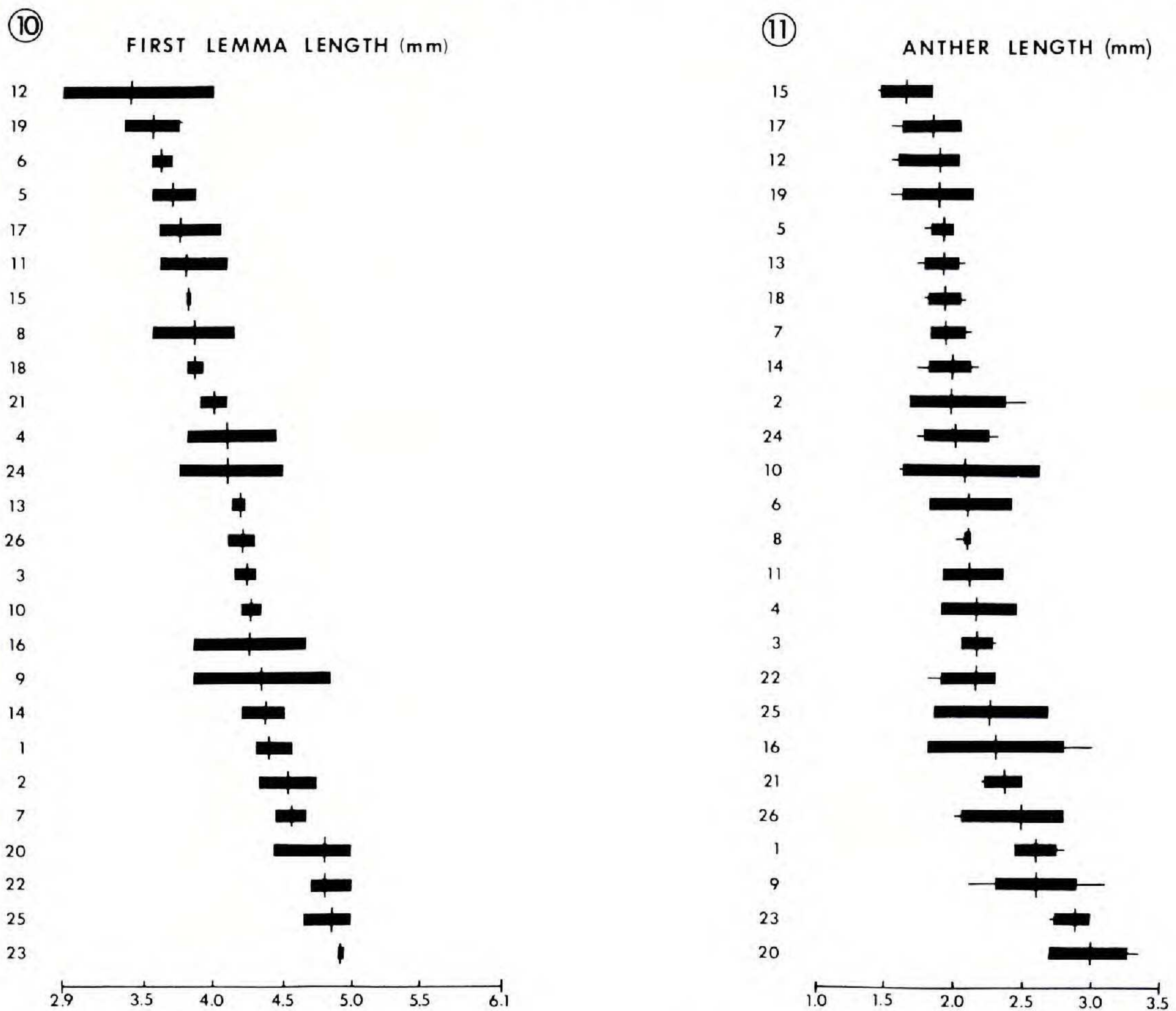
Histograms for some of the quantitative characters measured are shown in FIGURE 12. Comparison of these with FIGURES 2–11 shows that the range of



FIGURES 8, 9. Ranges of variation compared within and among populations: 8, first-glume length; 9, extent of lemma pubescence. Format same as in FIGURES 2, 3.

variation within each family is very high relative to the range of variation in the complex as a whole. For plant height the range within family 29 is 78 percent of that in the entire complex. The range for distance between the second and third panicle nodes is actually greater than that observed in the rest of the complex (1.5–6 cm vs. 0.6–3.6 cm). For many of the other characters, the range is between 38 and 62 percent of that of the whole complex. More important than the range of variation, though, is the distribution of values. Comparison of the ranges of values in the histograms of FIGURE 12 with those in the appropriate bar graphs of FIGURES 2–11 shows that the range of values in either family 29 or family 122 crosses most of the apparent breaks in distribution in the bar graphs. This is particularly true with such characters as extent of lemma pubescence (FIGURES 9, 12g), often considered to be of high taxonomic value in the genus.

Variation in each family could be entirely phenotypic, entirely genotypic, or some combination of the two. If all the plants were apomictically produced, they would be genetically identical, assuming no autosegregation or mitotic crossing-over. Although all the plants were greenhouse grown, the experiment was not controlled for small differences in environment. At the other extreme



FIGURES 10, 11. Ranges of variation compared within and among populations: 10, first-lemma length; 11, anther length. Format same as in FIGURES 2, 3.

the variation could be all genetic. If all the seeds were sexually produced, then they could all be genetically different. To sort out the phenotypic plasticity of these characters would require careful factorial experiments like those done by Davis (1983) in his study of *Puccinellia*. No matter how the variation is explained, however, it is still high enough to suggest that the characters are of minimal taxonomic value.

Could it be that, quite by accident, I happened on two unusually variable plants? Although possible, this seems unlikely. Plant 29 was collected from a crumbling basalt outcrop in northern Idaho, and plant 122 in a grassy meadow in north-central Oregon, both common habitats for *Poa secunda*; neither was part of an unusually variable population. Both plants were collected in 1978 and grown in a common garden for three years before being moved into the greenhouse early in 1981. The patterns of variation for many of the characters are strikingly similar for the two plants. Neither is consistently more variable from stem to stem than the other for all characters, and for such characters as spikelet and glume lengths, the ranges are virtually identical. It seems unlikely, therefore, that these results are simply accidental. The numerical analyses in the next section amplify and further support this conclusion.

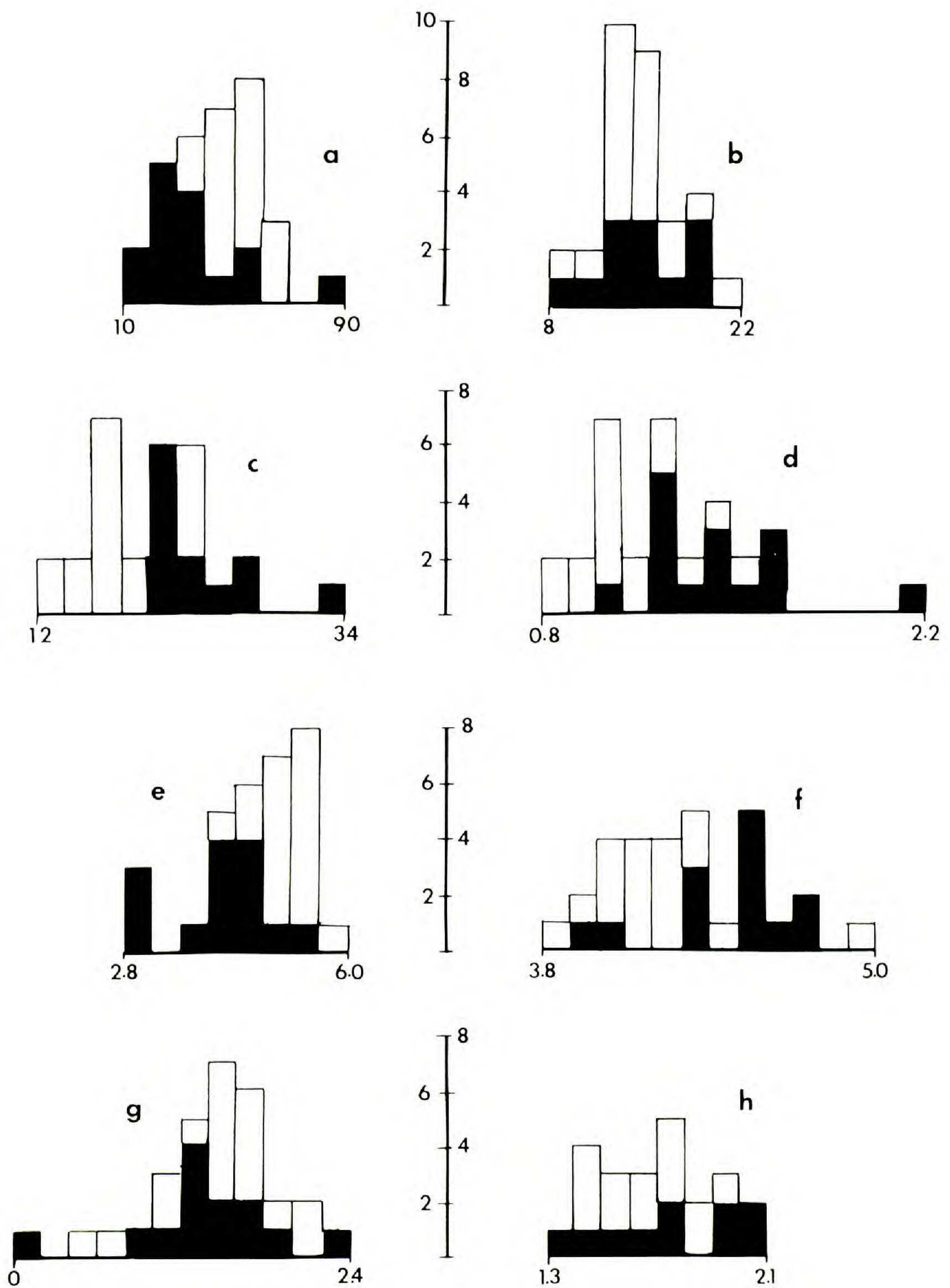


FIGURE 12. Histograms for 8 quantitative characters measured on 31 offspring of 2 self-pollinated plants: a, plant height (bar width = 10 cm); b, panicle length (bar width = 4 cm); c, basal-leaf length (bar width = 4 cm); d, leaf width (bar width = 0.1 mm); e, ligule length (bar width = 0.4 mm); f, first-lemma length (bar width = 0.1 mm); g, extent of lemma pubescence (bar width = 0.1 mm); h, anther length (bar width = 0.1 mm). Black bars = offspring of *Kellogg 29*, white bars = offspring of *Kellogg 122*; vertical scale = number of plants.

NUMERICAL TAXONOMY

Removal of all characters except those in which the range of variation is greater among than within populations leaves only 21 characters, the ranges of which still overlap among populations. The data described in the previous section suggest that many of these characters themselves are of questionable taxonomic value. Most of the key characters have been eliminated. Ligule decurrence is constant throughout the group. Sheath scabrousness and lemma pubescence vary as much within as between populations. Date of blooming (see next section), culm color, leaf involution and glaucousness, and—to a certain extent—plant height are all under environmental control. Of Hitchcock's eight original key characters, only panicle shape, ligule length and shape, and gross differences in height remain. There are 17 additional, non-key characters that are not automatically filtered out because of their variation pattern. This suggests three possible ways to describe and classify the complex: 1) four entities corresponding roughly to open-panicled plants, large plants, *Poa curtifolia*, and everything else, distinguished on the basis of combinations of the four characters mentioned above; 2) more than four entities, distinguished on the basis of characters other than those used in the past; or 3) one or more entities, none of which corresponds to previously recognized taxa.

UNIVARIATE STATISTICS. Both histograms and bar graphs show that no single character can be used to divide the complex. Histograms of the quantitative variables are mostly unimodal and approach normality, although a few are highly skewed; none is strongly bimodal. Four representative histograms, for all plants listed in APPENDIXES 1 and 2, are shown in FIGURE 13. Plants with extreme values for one character do not necessarily have extreme values for others. On the other hand, occasional aberrant individuals appear in which many of the parts are unusually large. When compared with many of the other plants, these stand out as strikingly different.

This pattern of variation also appears in the population samples illustrated in FIGURES 2–11. The order of populations, from lowest to highest mean values for each character, is not always the same. Furthermore, populations that are highly variable for one character are not highly variable in others, again suggesting noncorrelation of characters. The only exception is population 23, collected by C. V. Piper in the Grand Coulee, Washington, in 1900. This population is represented by three herbarium specimens that are all extremely large for most of the characters measured. However, because this "population" is a group of herbarium specimens with the same number, and because the range of variation in most characters is quite narrow, it may represent a single clump divided into three parts. Hence its extreme position should be treated cautiously (see also below).

BIVARIATE STATISTICS. Bivariate plots (see FIGURES 14, 15) show similar continua. Lemma pubescence and ligule length are two characters that have often been used in the taxonomy of the complex; they show, however, no perceptible groups. Other combinations of characters are similar. Although some characters such as plant height and panicle length are linearly correlated ($r = 0.8$), they

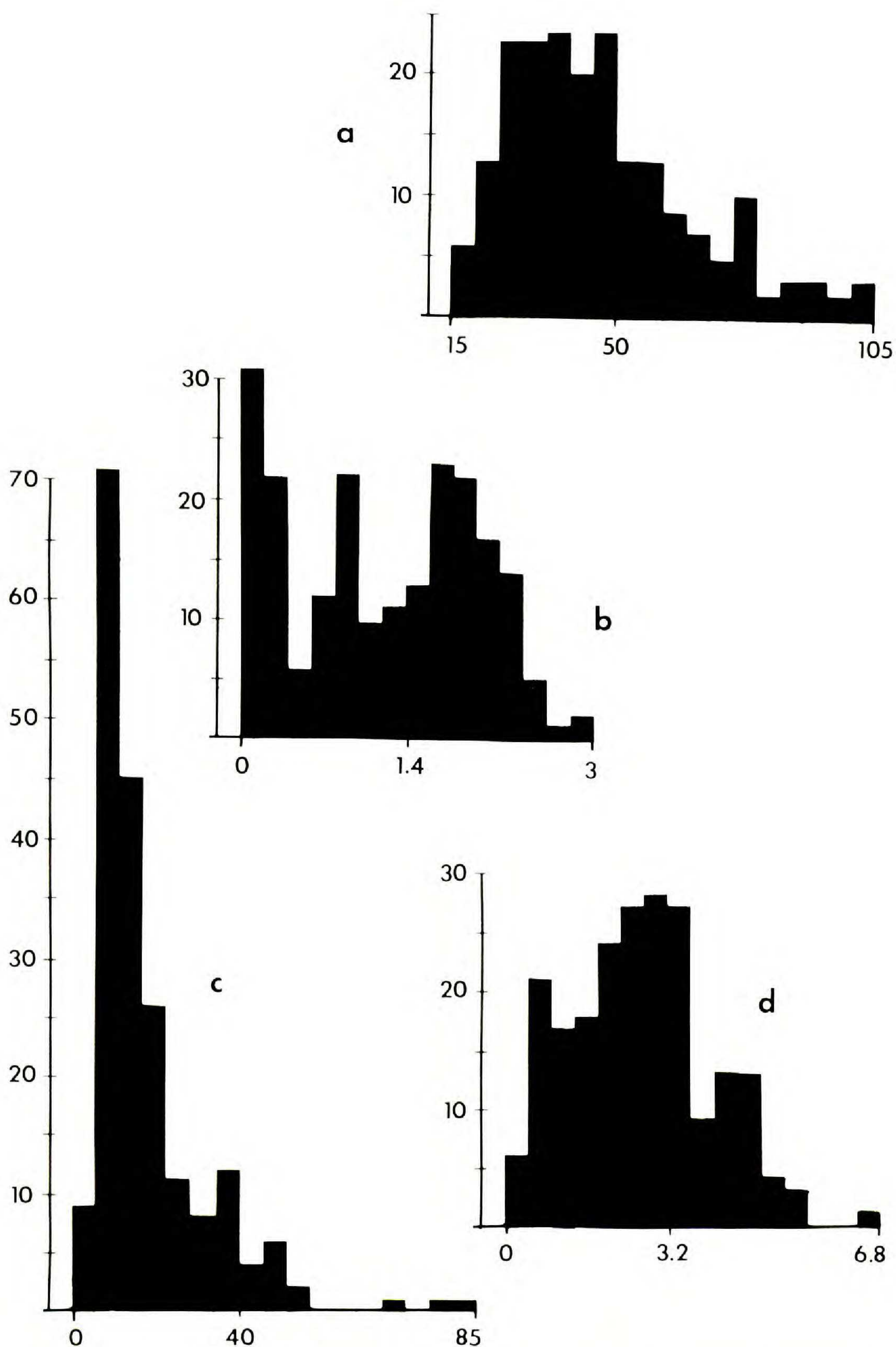
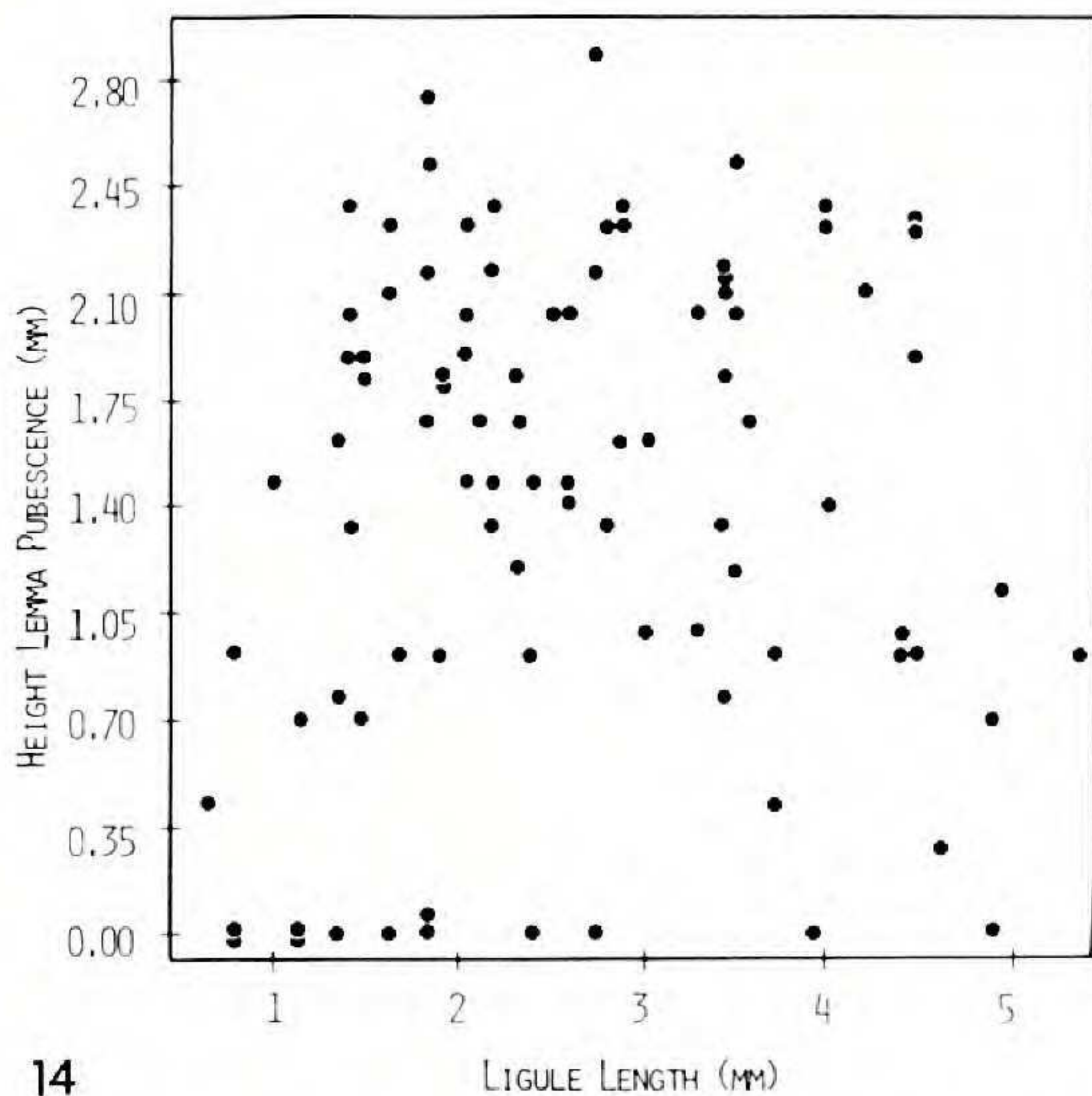
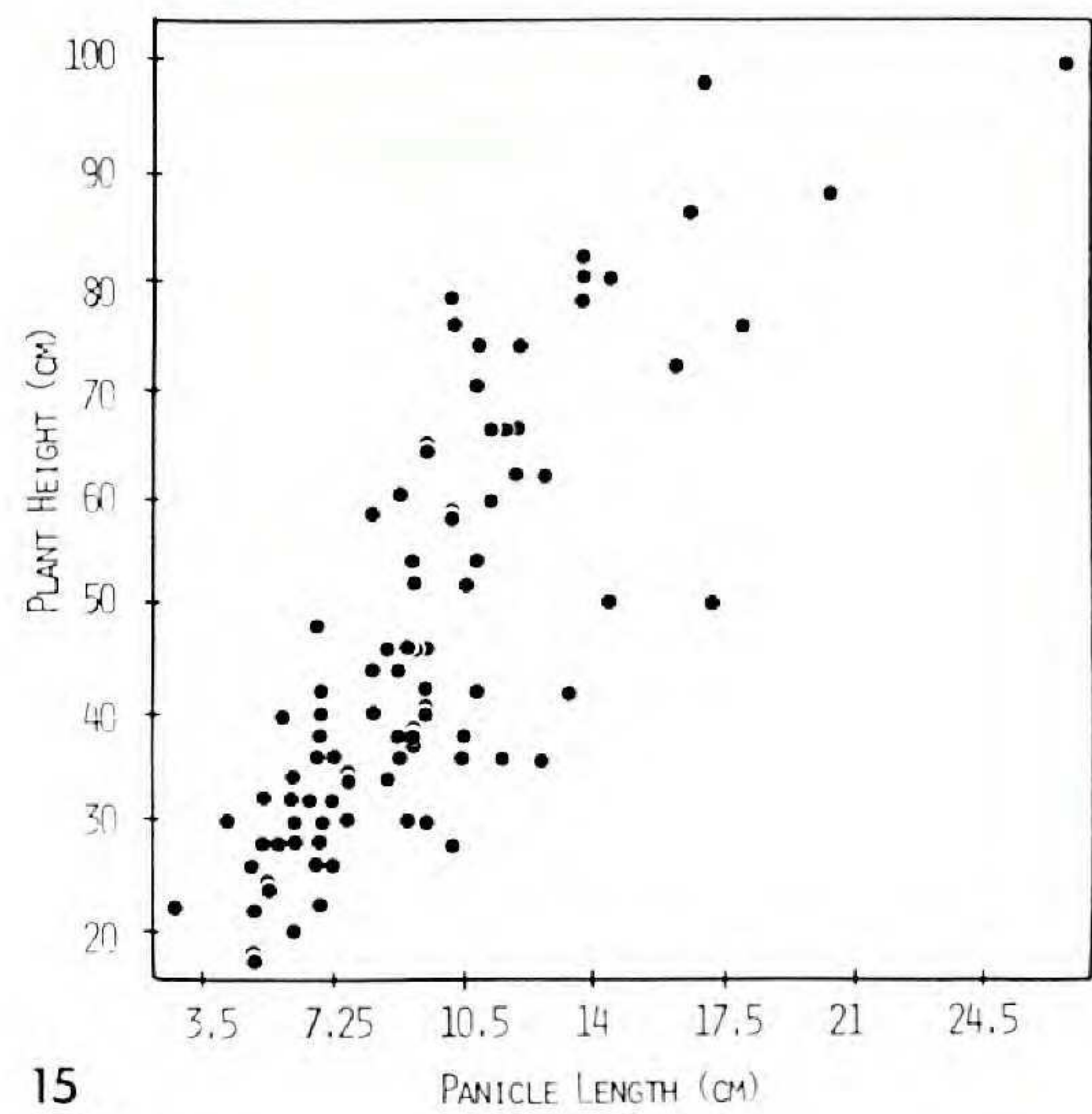


FIGURE 13. Histograms for 4 representative morphological characters measured on all plants in APPENDIXES 1 and 2: a, plant height (bar width = 5 cm); b, extent of lemma pubescence (bar width = 0.2 mm); c, basal-leaf length (bar width = 5 cm); d, lemma length (bar width = 0.4 mm). Vertical scale = number of plants.



14

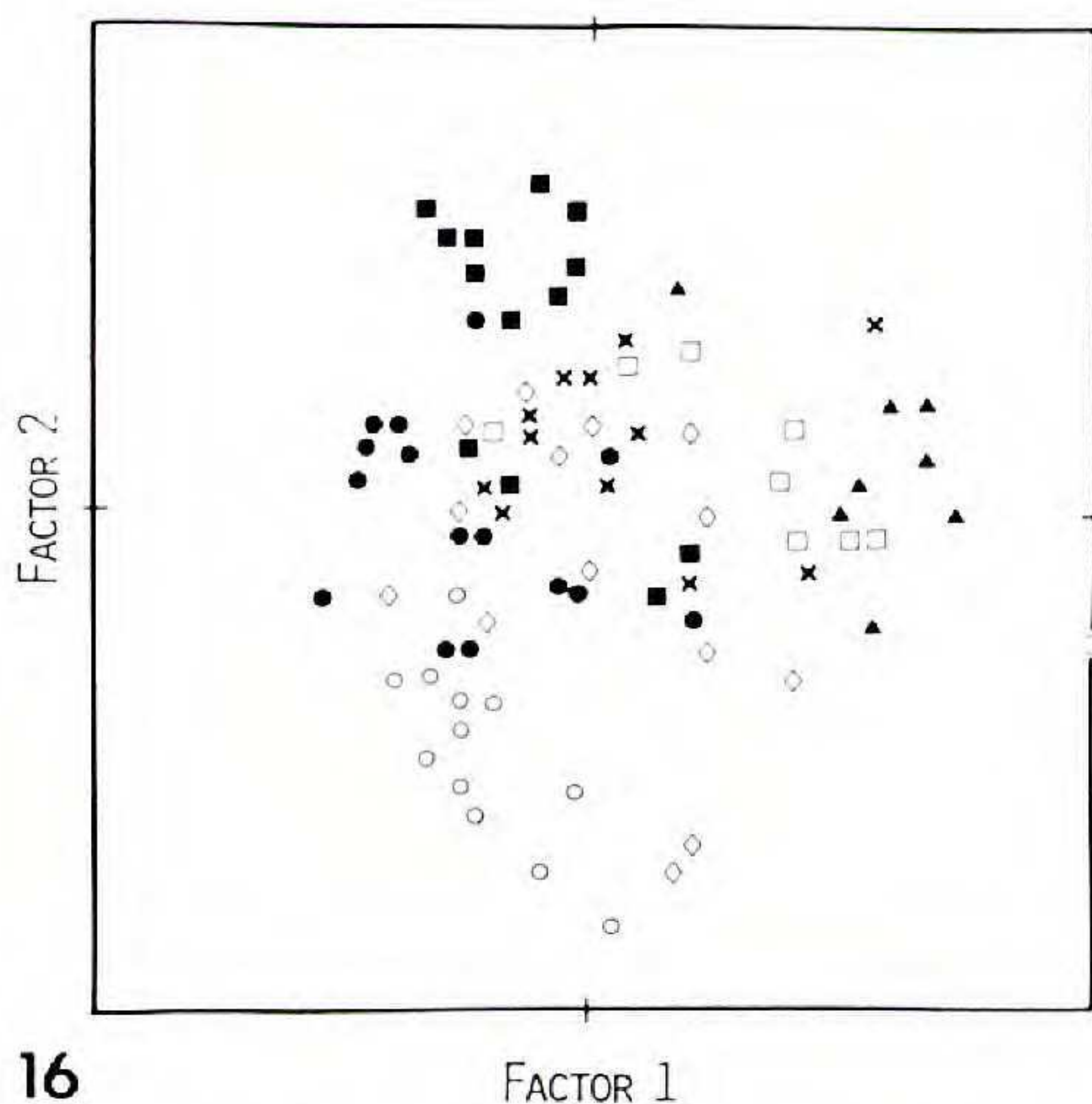


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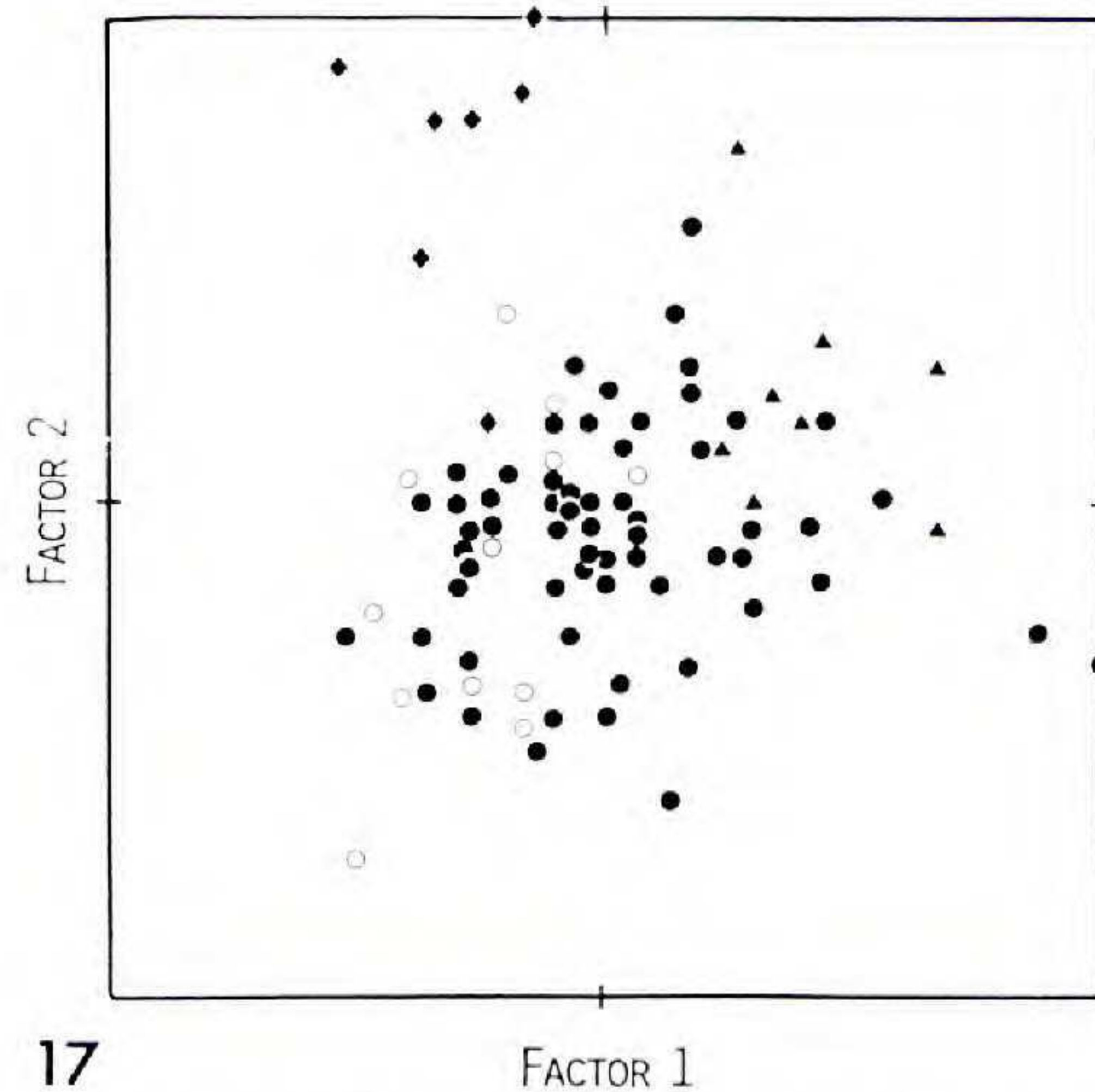
FIGURES 14, 15. Bivariate plots for plants listed in APPENDIX 1: 14, lemma pubescence vs. ligule length ($r = 0.087$); 15, plant height vs. panicle length ($r = 0.806$).

are not concordant and do not suggest any infrastructure for the group. It is more likely that the high linear correlation represents genetic linkage or similar developmental trajectories for the two characters.

PRINCIPAL-COMPONENT ANALYSES. A principal-component analysis on only the characters used by A. S. Hitchcock (FIGURE 16) shows that his taxa intergrade and that the single characters he used to define his species do not correlate with any other characters. The analysis using all 60 characters produced four notable results.

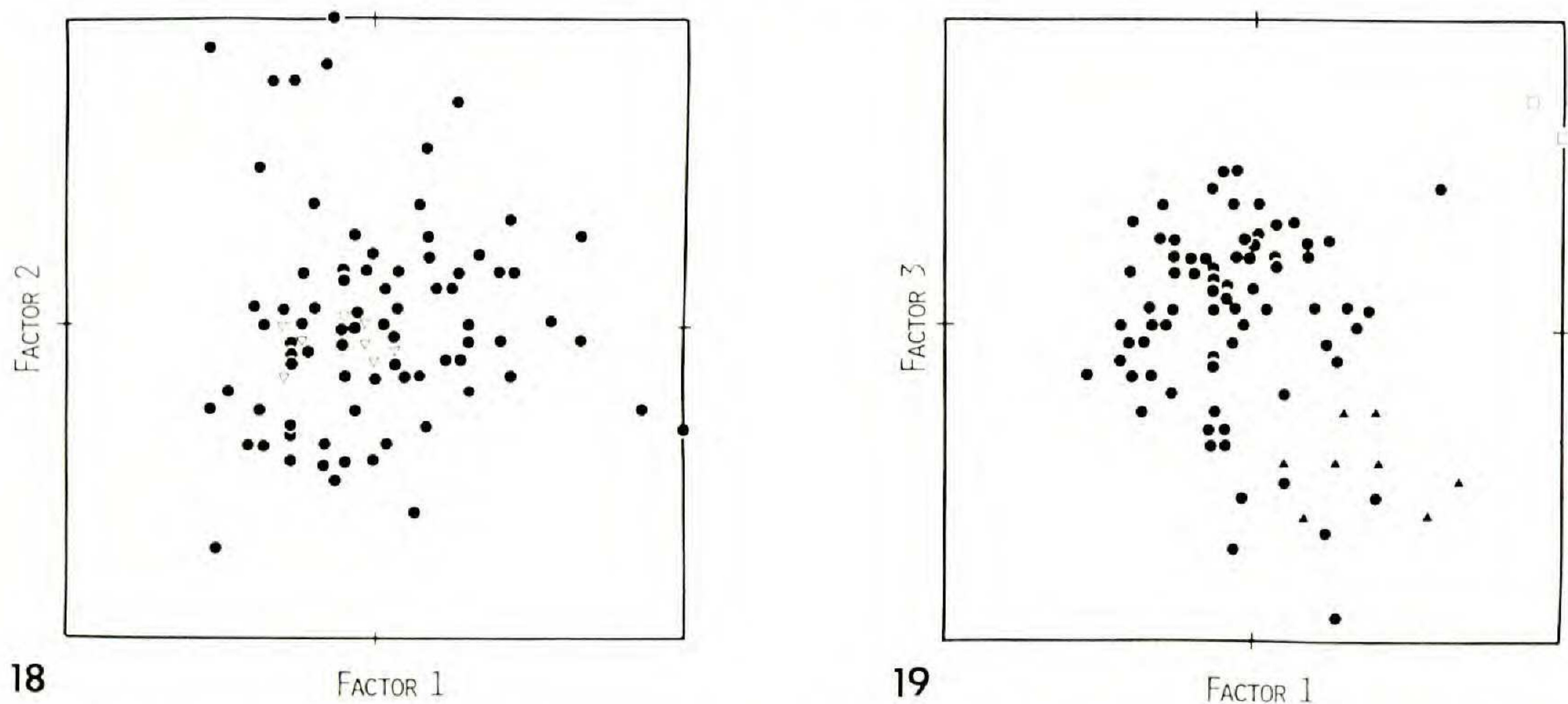


16



17

FIGURES 16, 17. Principal-component analyses: 16, A. S. Hitchcock's characters only (solid squares = *Poa scabrella*, open squares = *P. nevadensis*, solid circles = *P. sandbergii*, open circles = *P. gracillima*, open diamonds = *P. canbyi*, crosses = *P. juncifolia*, triangles = *P. ampla*); 17, all 60 characters (diamonds = *Poa curtifolia*, open circles = open-panicled plants, triangles = large plants with short ligules, solid circles = all other plants). Each axis = 6 standard deviations.



FIGURES 18, 19. Principal-component analyses: 18, all 60 characters (open triangles = separate culms of *Kellogg 56* scored as if separate plants, solid circles = all other plants); 19, all 60 characters, eliminating *Poa curtifolia* (triangles = large plants with short ligules, open squares = large plants with long ligules, solid circles = all other plants). Each axis = 6 standard deviations.

First, *Poa curtifolia* formed a more or less distinct cluster in the Factor 1 \times 2 plot, separate from the other plants (FIGURE 17). This result is particularly interesting in that the characters most distinctive of this species—leaf succulence and a white leaf margin—were not included in the data set. (See the following section for a discussion of leaf anatomy).

Second, the first three factors mainly represent size of vegetative features (characters 22, 39–42, 44–47), size of spikelet parts (characters 20, 52–59), and amount and distribution of trichomes (characters 14, 32, 33, 35). The first factor in particular thus probably includes a large environmental component. This is borne out by the fact that garden-grown plants tend not to cluster with field-grown plants from the same population.

Third, the individuals marked by open triangles in FIGURE 18 are actually separate culms of the same plant (*Kellogg 56*) scored as if they were separate individuals. They are scattered over about one and a half standard deviations in character space in most factor combinations, suggesting that variation within a single clone is large relative to that in the whole group.

Fourth, sixteen factors have eigenvalues greater than one, and the first three factors together explain only 39 percent of the variance. This is what one would expect if there were no definite groups and the OTUs all formed a nearly hyperspherical constellation in multidimensional space. Examination of the first three principal-component axes on the three-dimensional visual display created by Huber and his graduate students (see Kolata, 1982) shows that the constellation of points is actually more or less L- or T-shaped. Most of the plants form a dense cloud that is the bar of the T; individuals classified as *Poa curtifolia* plus the plants with extremely large values in several characters form a more diffuse “tail.” Some of the large plants fall as far from the dense part of the cloud as do members of *P. curtifolia*.

I examined plots of all possible two-way combinations of the first ten factors and found no pattern any more interpretable than those shown. The open-panicked plants are closest together in the plot of factor 1 vs. factor 5, but even so they do not form a discrete group.

Eliminating the characters that vary within the plant and those that are clearly under environmental control reduces the total number of characters to 48—29 quantitative and 19 qualitative. This changes the results only slightly. The first three factors now explain 43 percent of the variance. The relationships of most plants to each other remains similar, although *Poa curtifolia* is somewhat more distinct. The results of the analysis with quantitative characters only are also similar to those in the other analyses.

When *Poa curtifolia* is eliminated from the analysis, the first three factors explain 45 percent of the variance and some weak groups appear in the plot of Factor 1 \times 3 (FIGURE 19). The group in the lower right corner of the graph includes mostly large plants with relatively short ligules. Factor loadings remain similar to those in the other analyses. The two plants in the upper right corner, shown by open squares, appear together in all analyses and are always distant from the rest of the group. These plants both have extremely large panicles on very long culms. Reference to the bivariate plot of plant height vs. panicle length (FIGURE 15) shows that the two plants (the rightmost points) are indeed extreme and may have slightly unusual proportions of those parts. Although the two plants are morphologically quite similar, they were collected nearly 600 miles apart and on very different sites, one near Reno, Nevada, the other in the Wasatch Mountains of Utah. Again, this suggests that the very largest plants are simply isolated extreme forms.

DISCRIMINANT ANALYSES. In the first of these analyses (shown in FIGURE 20), plants of population 23 (from eastern Washington—far left) appear radically different from the large plants in populations 21, 22, 24, and 25 (center), which are in turn distinct from the rest of the group. *Poa curtifolia* (populations 29 and 30) is less well separated than by the principal-component analysis. The open-panicked populations, the Gaspé populations, and the California group all cluster together. The greatest discrimination is provided by the first canonical variable, which is primarily a function of basal-leaf length, flag-leaf length and height, leaf width, and ligule shape. Characters loading on axis II are length of the flag leaves, the panicles, the first glumes, the lemmas, and the anthers, width of the leaves, and extent of pubescence on the lemmas.

As noted earlier, population 23 is an outlier in terms of most characters; furthermore, it may represent not a population but a single clump (clone). Removing it from the analysis produces the picture shown in FIGURE 21. Again the large plants of populations 21, 22, 24, and 25 are distinct, although not as dramatically so as in the first analysis. *Poa curtifolia* is now clearly separate. The other populations in the right-hand group overlap; the jackknife procedure²

²A procedure whereby an OTU is removed from the data matrix and the discriminant functions are recalculated. The OTU is then entered into the new discriminant functions and is classified accordingly. This is done for each OTU in turn. If the group to which the OTU was initially assigned is discrete from the other groups, then the OTU will be reassigned to the group from which it came.

produces frequent misclassifications, suggesting little discrimination among them. Thus, in a procedure designed to maximize distances among populations, there are only three clear groups formed: *P. curtifolia*, large plants, and everything else.

The cloud of points in FIGURE 21 is roughly T-shaped, with the large plants forming a more or less diffuse tail. Virtually all discrimination is on the first canonical axis, which—like the first principal-component axis—represents size of vegetative parts. The variables with the highest F-values are the lengths of both basal and flag leaves. Removal of these from the analysis produces essentially the same picture, with the large plants now being distinguished on the basis of the short ligule. Because of the bias in the sample, these results are good evidence for the conclusions that panicle shape is not concordant with any other character, and that plants with open panicles do not form a discrete group. The same bias, however, means that this analysis does not provide good evidence for formal recognition of large plants with short ligules; large plants with long ligules were not included in the analysis. Thus, principal-component analyses give a weak argument for lumping these large plants with the rest of the complex, while discriminant analyses provide an equally weak argument for maintaining them as distinct. Other data on population structure and distribution give no rationale for recognizing them as a separate taxon.

OTHER CHARACTERS

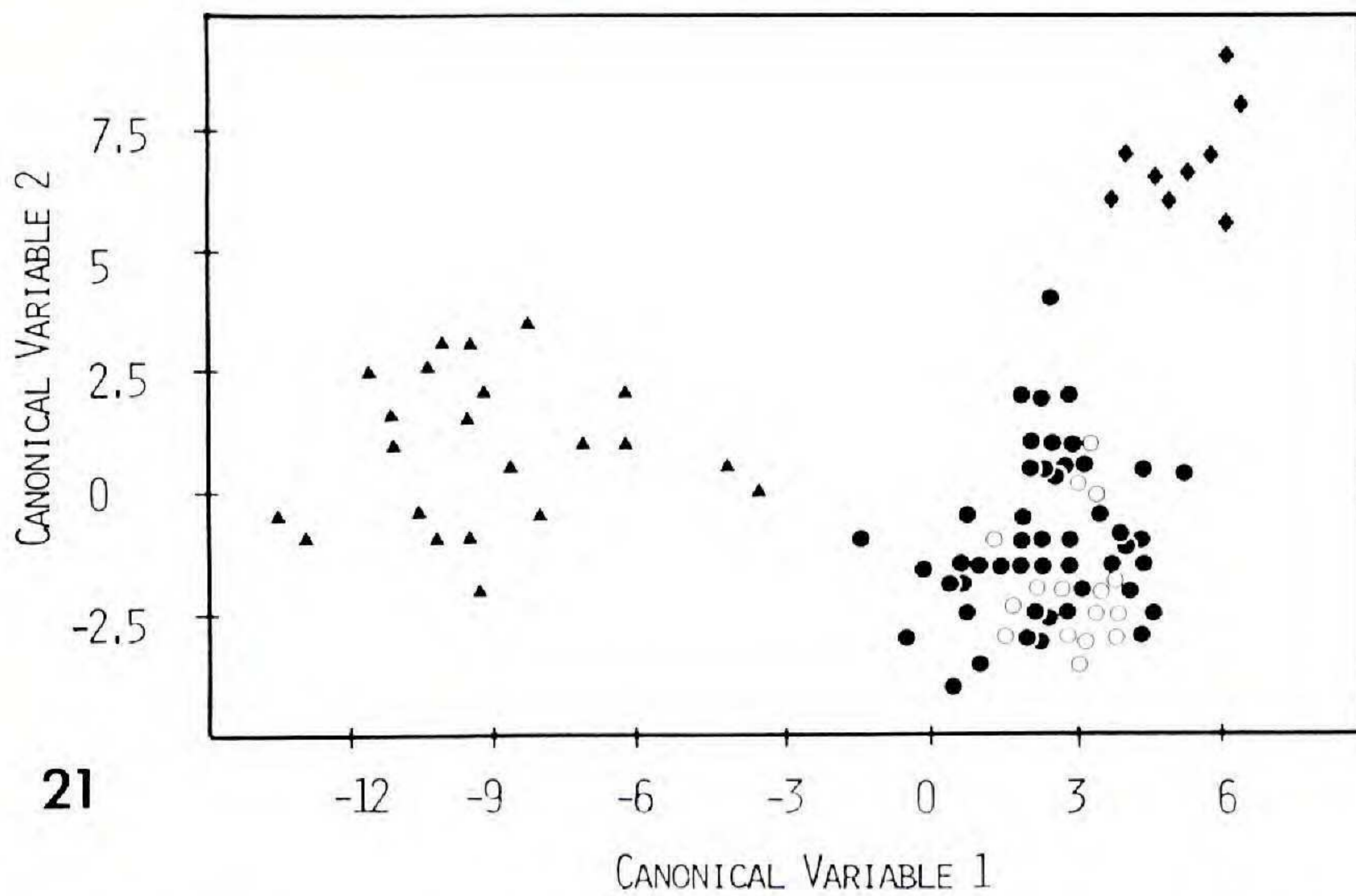
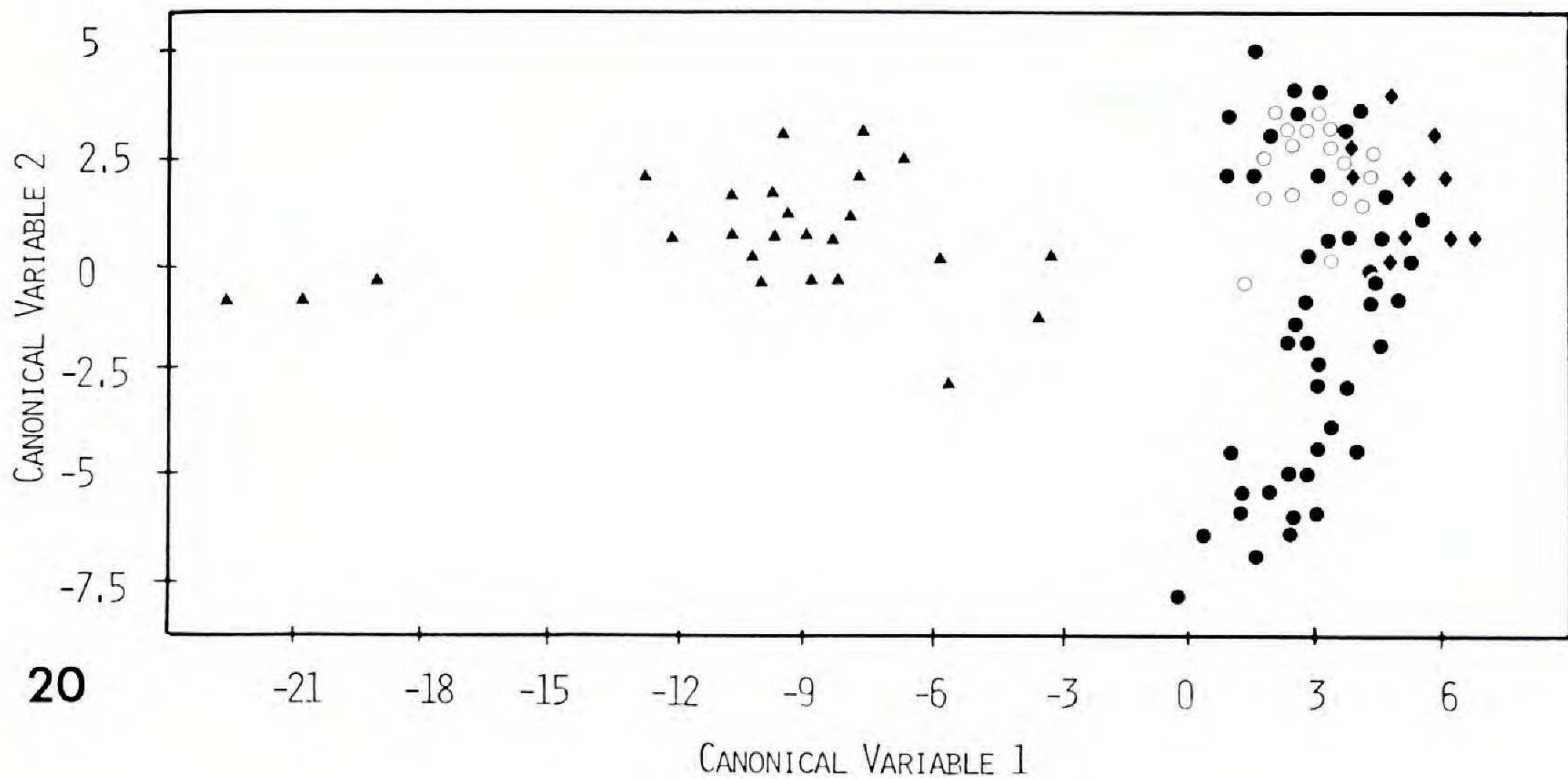
Extensive analyses of gross morphology have shown that the *Poa secunda* complex is made up of only two taxa. This conclusion is supported by data on phenology, leaf anatomy, and ecology.

PHENOLOGY

Both C. L. Hitchcock and co-workers (1969) and Cronquist and colleagues (1977) have used phenology as a taxonomic character, separating species into those that bloom in April, May, or June vs. those that bloom in July or August. Date of blooming in the wild, however, appears to correlate more with altitude and habitat than with morphology: plants consistently bloom in the early part of the growing season and then become dormant.

I followed marked plants in two natural populations near Moscow, Idaho, and observed two apparent peaks of blooming time, about three to five days apart, with each totaling about ten days. The early-blooming plants seemed to be somewhat smaller and to have smaller, narrower leaves than the later ones. Unfortunately, the numbers of plants observed were too small for any statistical tests of these observations.

Plants from a variety of provenances, when grown in the experimental garden, bloom within a period of 17 days; plants forced in the greenhouse bloom within four weeks of being brought indoors. Blooming time is thus not a good diagnostic character. In general, in both garden and greenhouse, specimens of *Poa curtifolia* are some of the earliest plants to reach anthesis, and the large plants that traditionally would have been assigned to *P. ampla* are among the latest.



FIGURES 20, 21. Discriminant analyses: 20, 18 characters and all plants listed in APPENDIX 2; 21, 18 characters and all plants listed in APPENDIX 2 except population 23 (diamonds = *Poa curtifolia*, open circles = open-panicked plants, triangles = large plants with short ligules, solid circles = all other plants).

If plants are assigned to Hitchcock's taxa and time to anthesis is compared among all taxa by analysis of variance, the earliest species is found to be significantly earlier than the latest. Because this represents the average time to anthesis, however, and because there is still considerable overlap among all the ranges, statistical significance may not indicate biological significance. The weak tendency for time of anthesis to correlate with plant size is shown in FIGURE 22.

ANATOMY

Cross sections of leaves show that members of the complex are anatomically variable (FIGURE 23). All plants have double bundle sheaths and a row of

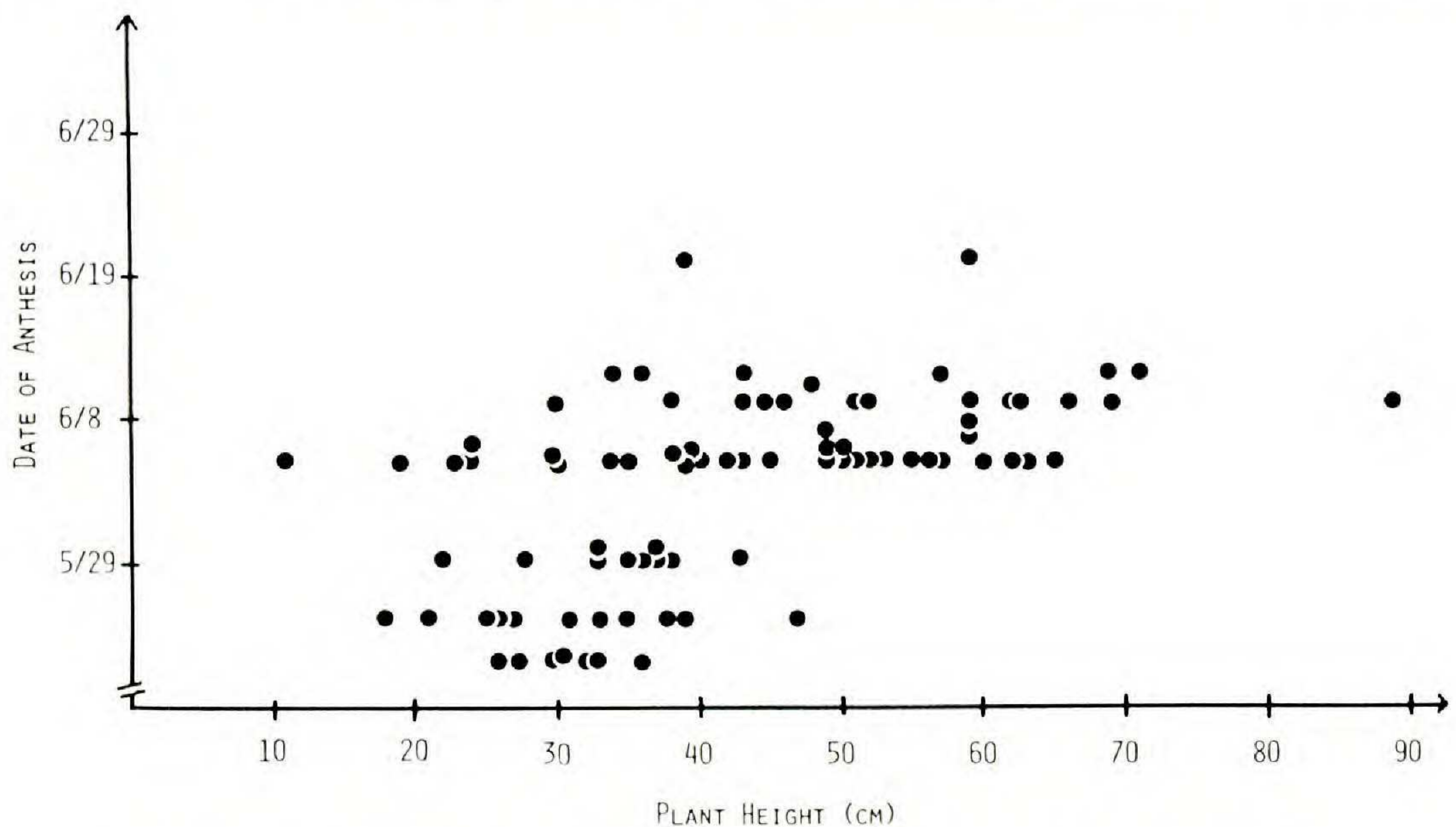


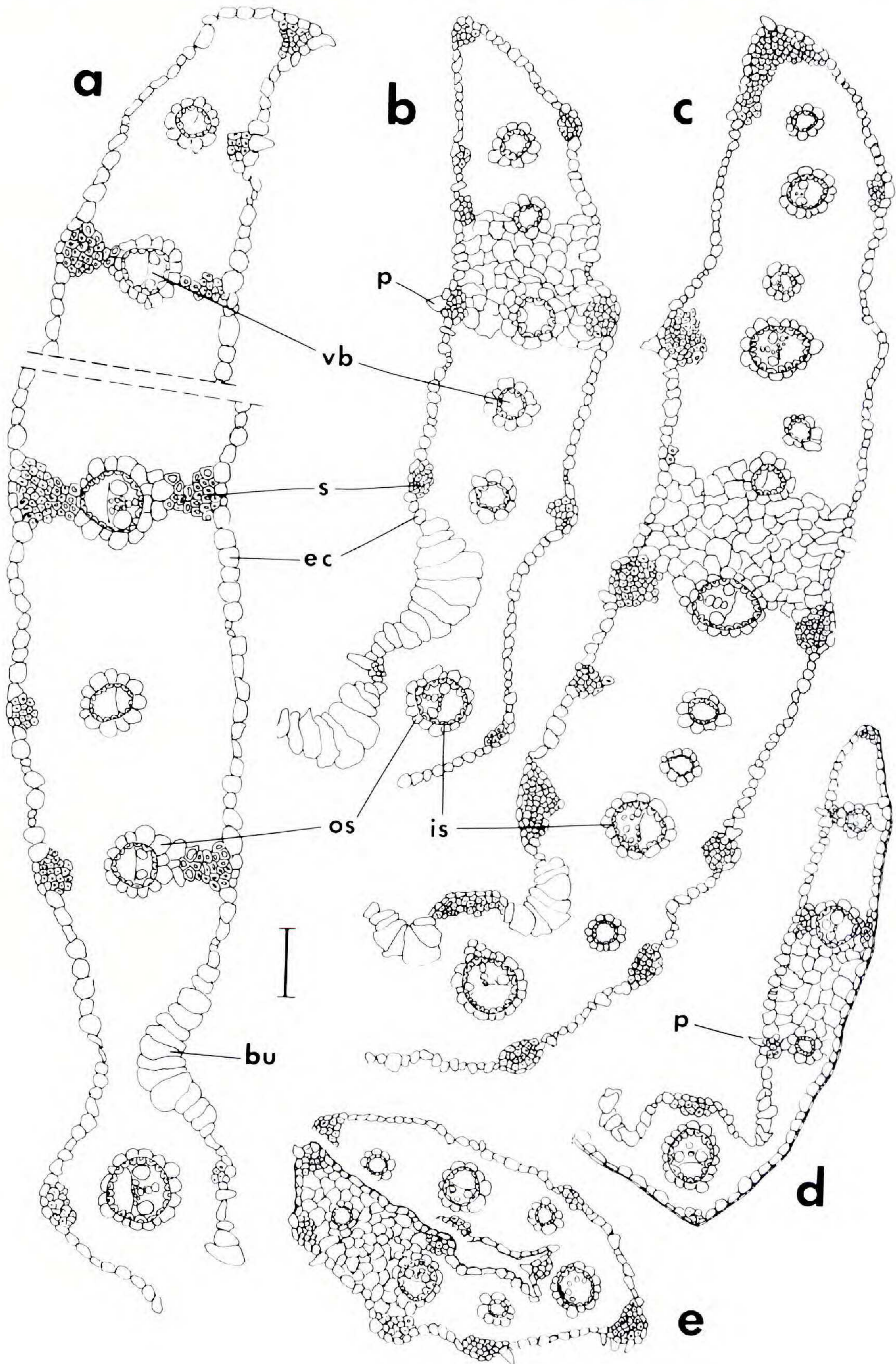
FIGURE 22. Bivariate plot of date of anthesis vs. plant height ($r = 0.45$).

bulliform cells on both sides of the midrib. Plants differ primarily in the amount of sclerenchyma and in the shape of the epidermal cells. Although many plants have the major vascular bundles fully embedded in sclerenchyma, others have sclerenchyma not connected to the vascular bundles, and some have the sclerenchymatous region reduced to only a few cells. The amount of sclerenchyma seems to correlate with the moisture level of the site, being much greater in plants grown on drier sites. Relative amount also varies when plants are moved from field to experimental garden, which also suggests environmental influence. The epidermal cells may be somewhat flattened in cross section, in which case there is generally a thick cuticle, or they may be more rounded and irregular with a thinner cuticle. In some plants the adaxial surface has rounded epidermal cells and the abaxial epidermis has flattened ones. Epidermal peels from a sample of 20 plants were all similar, with sinuous-sided silica bodies and parallel-sided subsidiary cells. Leaf anatomy thus conforms to the standard festucoid pattern (as described in Gould & Shaw, 1983), and the variation that occurs does not correlate with other characters.

SUBSTRATE

Members of the complex grow on a variety of substrates, generally on neutral to strongly alkaline soils, sometimes with high amounts of soluble salts. Plants

FIGURE 23. Cross sections of leaves showing range of variation in complex: a, *Kellogg 154* (Oregon; large plant with short ligules and nearly glabrous lemmas, greenhouse grown); b, *Kellogg 226* (central Idaho, open-panicked plant with long ligules, greenhouse grown); c, *Kellogg 227* (*Poa curtifolia*, central Washington); d, *Kellogg 263* (Oregon,



open-panicled plant with short ligules); e, *Kellogg 210* (Idaho, alpine plant with long ligules and pubescent lemmas). Scale = 0.1 mm; s = sclerenchyma; vb = vascular bundle; os = outer bundle sheath; is = inner (mestome) sheath; bu = bulliform cells; ec = epidermal cells; p = prickle hair.

with open panicles and short ligules occur only on the walls of wet, mossy gorges near Multnomah Falls above the Columbia River in Oregon; those with open panicles and long ligules are montane and usually grow in crevices in granite. Large, glaucous plants are often but not always found in apparently saline basins. These generalizations about ecology do not hold up to close inspection, however. To see if any edaphic characters correlated with morphology, I ran three multiple regressions of seven soil characteristics against basal-leaf length, ligule length, and lemma length (three characters shown by numerical taxonomy to be important in describing the total variation in the group). R^2 values are 0.092, 0.296, and 0.127, respectively, for all combinations of soil characters with the three morphological characters. Edaphic factors are thus taxonomically uninformative.

Poa curtifolia is the one exception, being restricted to serpentine soils in the Wenatchee Mountains of central Washington. Other members of the *P. secunda* complex are also found on serpentine soils, but they are not morphologically distinct.

REPRODUCTIVE BIOLOGY

The *Poa secunda* complex has long been known to be apomictic (Nygren, 1951), and apomixis has been widely used to explain morphological variability in the group. Early in my studies of the reproductive biology of the group, I developed a hypothesis, based on some sketchy preliminary data, that some of the more distinctive morphs (like the large, short-liguled plants) were more highly apomictic than the other members of the complex. This hypothesis not only proved to be wrong but also was based on a logical flaw that I will discuss briefly below.

Bagging experiments showed that pollen is necessary for seed set; apomixis, when it occurs, must be pseudogamous. All plants set seed when self-pollinated. From 2721 attempted crosses I produced 4 apparent hybrids; other offspring were morphologically indistinguishable from the maternal parent and so were presumed to be apomictic. The parents of the hybrids were very different morphologically. This suggests that if there are fertility barriers, they are not between forms that are highly morphologically differentiated. These results are confirmed by the much larger studies of Hiesey and Nobs (1982). Thus, sexual reproduction can and presumably does occur even between very different morphs.

To determine the extent of apomixis in individual plants, I cleared ovules in Herr's solution and observed them with Nomarski optics (see Kellogg, 1983; Greene, 1984). In each of 25 plants, I scored up to 50 ovules as being sexual or potentially apomictic. The percentage of apomictic ovules varied from 25 to 100. It varied as much as 40 percent among plants collected from the same locality, and percentages from the same plant in subsequent years are also quite different. Percent apomixis in parent plants did not correlate with that in the offspring. This variation in percent apomixis does not reflect variation in pollen stainability; although highly apomictic plants are usually mostly pollen sterile,

pollen-fertile plants may exhibit any amount of apomixis. Like percent apomixis, percent pollen stainability varies widely with the environment. It is not correlated with regularity of meiosis.

Chromosome number is likewise variable. *Poa curtifolia* has $2n = 42$. Other members of the complex have numbers varying from $2n = 44$ to $2n = 106$ (Hartung, 1946). Many of the largest plants are 9-ploid, but some have higher or lower numbers, and not all 9-ploids are large. Thus, chromosome number is not associated with morphological variants.

Were they morphological characters, the aspects of reproductive biology that I have investigated would be ruled out as taxonomically unimportant. Some, such as interfertility, do not vary within the group. Others, such as percent apomixis and percent pollen stainability, are highly variable depending on the environment, but even if they were stable, they would be of no use in explaining the morphological variation since they do not correlate with any aspect of morphology. Because of this lack of correlation, there is no way in which I can conclude that the morphological complexities exist *because of* apomixis. My initial hypothesis of the unusual morphs being more highly apomictic than the more widespread ones has thus proved to be wrong, but even had it been correct, it would have been an inadequate explanation for the morphological variation. The only way apomixis can maintain a particular form is if it is obligate. If there is any recombination at all (and the production of a small number of hybrids suggests that there is), then the plants are effectively sexual in terms of their ability to generate variation. In the case of facultative apomixis, the process of recombination is slowed but by no means stopped (see discussions by Marshall & Weir, 1979, and Lynch & Gabriel, 1983).

DISCUSSION AND CONCLUSIONS

In general, my work suggests that much of the presently accepted taxonomy of the genus *Poa* is suspect. The amount of population-level variability in the *P. secunda* complex is not unique in the genus. The genus contains several widespread polymorphic taxa, including *P. pratensis*, *P. alpina*, *P. arctica*, and *P. glauca*, in which one to many species are commonly recognized. All include numerous entities that have been given specific status at some time in the past, and all are circumboreal, apomictic, and with aneuploid chromosome numbers suggesting some ancestral hybridization. Although characters that are variable in one part of the genus may still be taxonomically useful in another, such characters, once shown to be unreliable, should not be used blindly. Overreliance on one or a few gross morphological characters may have caused unnecessary splitting, producing artificial morphological entities rather than biological ones. Studies of other bluegrasses must consider the possibility that many traditionally used characters are unreliable. Lemma pubescence is heavily relied upon to separate species or sections throughout the genus. However, the amount of lemma pubescence often varies greatly within populations in *P. secunda* and among the offspring of a single self-pollinated plant; it also varies in populations of *P. curtifolia*, a narrowly endemic species. This character must

thus be used carefully. Similarly, I have shown leaf folding to be controlled by soil moisture, yet a number of bluegrass species are distinguished by such features as folded or involute leaves. In other groups the value of this character can only be verified by common garden studies.

Included in the first multivariate analyses were several plants from species outside of the complex. On the basis of the characters used in the analyses, however, they did not appear distinct from other members of the group. This suggests that other taxa in the genus may prove, on closer examination, to be poorly delimited and, like the members of the *Poa secunda* complex, part of a continuum of variation.

Panicle shape has no taxonomic value in this complex. Plants with panicles that remain open after anthesis were formerly known as *Poa gracillima*. They often occur in granite outcrops, frequently at high altitude, in the northern Rocky Mountains and the Sierra Nevada, as well as in Chile (Arnold, 1981). The character state persists even in garden-grown plants. The preceding analyses have shown, however, that this character state does not correlate with any others. Open-panicled plants are shown by triangles in the scatter diagrams; it is obvious that they intergrade completely with other members of the complex on the basis of all characters but this one.

Several hybrids were produced in crosses of open-panicled plants with narrow-panicled ones. The F_1 s had panicles that were narrow at the top, but the bottom two branches remained at an angle of about 30° to the rachis after anthesis. Such a plant would be classed by most taxonomists as having a narrow panicle, and its morphological intermediacy would probably go undetected. Thus, populations comprising plants with genes for both open and narrow panicles may not be recognized.

Poa curtifolia is morphologically distinct, based on the characters used in the numerical analyses. Not included, however, were the facts that it has thick, almost succulent leaves often with a prominently white margin, it is restricted to serpentine soils in the Wenatchee Mountains of Washington, and its chromosome number is $2n = 42$, with good pairing at meiosis. It should therefore continue to be recognized as a species distinct from the rest of the complex.

Many of the very largest plants are separated from the rest of the complex because of gaps in relative sizes of parts. These unusually large plants are geographically isolated from each other, with neither distinct ecological requirements nor a discrete range. I have never found them growing in pure stands. Either they grow with smaller members of the complex, or they occur as isolated plants in ditches or on cut-banks. What these forms represent biologically is still an unanswered question. Because sexual reproduction can and presumably does occur in the group (Kellogg, 1983), they may be simply unusual segregants that happen to be particularly vigorous on extreme sites. This contention is supported by the data presented under Results: among the offspring of a single self-pollinated plant, some had extreme values for certain characters. Unusually large plants may thus be produced fairly commonly.

In their most striking form these large plants, most of which would traditionally be put into *Poa ampla*, have short ligules, little lemma pubescence,

and very glaucous foliage, but their most distinctive character is their long leaves. In FIGURE 3, which represents a univariate display of basal-leaf length, there is a break at about 20 cm separating the large plants. The histogram for this character (FIGURE 13C), however, shows little reason to define groups in this way. Also, the histogram in FIGURE 12C shows that the offspring of a single self-pollinated plant vary across the apparent break. Increasing the sample size obscures even the univariate pattern.

Some taxonomists might still prefer formal recognition of these plants at the varietal level at least. Such plants are most valuable as forage grasses, which sets them apart from the other members of the complex that are largely ignored by cattle. Cattle graze by wrapping their tongues around the leaves of the plants they eat and so prefer plants with long basal leaves. Cows can therefore "recognize" *Poa ampla* as distinct from the rest of *P. secunda* because of the leaf length, a character with a nearly continuous distribution. Formal recognition of *P. ampla* would thus be arbitrarily dividing the continuum of basal-leaf length so as to create a special-purpose classification reflecting the mouthparts of cattle. Continuity of variation makes it unjustifiable to recognize these forms taxonomically.

The *Poa secunda* complex is made up of many fewer taxa than previously described. In this study I have defined a species as a group of plants with similar morphology and with no obvious morphological gaps in sets of concordant characters. Only *P. secunda* and *P. curtifolia* adequately fit this definition. Such taxa as *P. sandbergii*, *P. canbyi*, *P. scabrella*, and *P. incurva* can be confidently placed in synonymy. The characters on which they were based either vary at the level of the clone or population or are almost completely under environmental control. Furthermore, no other characters were found that distinguish groups within this part of the complex. The search for taxonomically useful patterns in *P. secunda* has shown that no characters are concordant—i.e., that no characters define nonoverlapping sets of plants. In other words, a species is a cluster of points in taxonomic hyperspace, where the dimensions of the space are broadly defined to be any set of characters; in this case the characters are predominantly morphological ones. *Poa secunda* can be described as a sort of minimal species; at the very least we can make generalizations of the form "plants with character X will also have character Y." This is the rationale for not considering *P. gracillima* as a separate species even though it can be discriminated on the single axis representing open vs. closed panicles. Knowing that the plants have open panicles still does not allow even very trivial generalizations.

Such a conclusion also means that, at our current level of knowledge, we can make no claims about evolution within *Poa secunda*. Because there are no characters that can serve as evolutionary "markers," we cannot evaluate the various processes that might have generated the pattern. Hypotheses of fusion of disparate lineages by hybridization, although appealing, are merely plausible suggestions, not subject to test. The roles of polyploidy and apomixis cannot be evaluated. The pattern of variation, in other words, does not illuminate the historical pattern of microevolutionary processes.



FIGURE 24. *Poa curtifolia* and *P. secunda*. a, *P. curtifolia*, habit (Kellogg 227), $\times 0.35$. b–m, *Poa secunda*. b, habit (Kellogg 56), $\times 0.35$. c–f, variation in lemma size and pubescence, all $\times 3.5$: c, Stevens 1208 (DAO); d, Hitchcock 11301 (US); e, Ward 488 (US); f, Maguire 13874 (DAO). g, open panicle (Kellogg 226), $\times 0.35$. h–m, variation in ligule size and shape, all $\times 3.5$: h, Kellogg 214; i, Kellogg 114; j, Kellogg 222; k, Kellogg 36; l, Kellogg 274; m, Kellogg 101. Complete specimen citation in APPENDIX 1.

Poa secunda has been delimited on phenetic, not cladistic, grounds. Although it can be distinguished from other members of the genus by a combination of characters, there is no reason to believe that any of these characters is uniquely derived. As noted at the outset, the only possible apomorphies for the group

are shape of the spikelet and length of the first rachilla internode, and even these are not unique to *P. secunda*. Other characters, such as caespitose habit and perfect flowers, may be plesiomorphic and therefore not indicative of phylogenetic relationship. Still others, such as lack of a lemma web, may be either plesiomorphic or convergent. The group is thus not demonstrably monophyletic *sensu* Hennig; monophyly could only be determined in the context of a phylogeny for the entire genus. Quite possibly other species should be included in a group united by long spikelets and rachilla internodes; *P. secunda* may thus be paraphyletic. To try to define a species within the complex as the smallest strictly monophyletic unit (see Mishler & Donoghue, 1982) seems unworkable, given the distribution of characters. The basic model of cladistics does not apply to hybridizing groups; the apomorphies of the parental lines become hopelessly blended, lineages cannot be identified, and the application of concepts of strict monophyly seems inappropriate. The definition I have used for a species, therefore, not only prevents analysis of evolution within *P. secunda*, but also analysis of evolution between *P. secunda* and other parts of the genus.

I have thus chosen to recognize formally only morphological units within which all characters vary and covary continuously. There are no gaps in the distribution of the characters, and most are uncorrelated. Such units do not reflect anything about phylogeny. Given the current state of classification and knowledge of characters in *Poa*, such a species concept may be the only one that can be applied with any consistency.

The foregoing points all lead to the conclusion that there is only one defensible taxonomic treatment for the group: to recognize *Poa curtifolia* and to include everything else in *P. secunda*. Variation in many characters is indeed complex, both at the level of the species (*P. secunda*) and also apparently at other levels. To impose any taxonomic structure would obscure, rather than illuminate, the pattern.

TAXONOMIC TREATMENT

Poa curtifolia Scribner, Circ. U. S. Div. Agrost. **16**: 3. 1899. TYPE: Washington, Kittitas Co., Cascades, Mt. Stuart, Aug. 1878, *Elmer 1148* (holotype, us!). FIGURE 24a.

Plants 2–5 dm, caespitose to short-rhizomatous, glaucous; branching intravaginal; culms 0.5–0.8 mm thick below inflorescences, sometimes becoming red with age. Basal leaves 3–8 cm × 0.5–2.5 mm, the blades extending almost at right angles from sheath, flat, more or less fleshy, with prominent white marginal vein, scabrous on margin only. Flag leaves 0.5–2 cm × 0.2–2.6 mm, borne well below midpoints of culms. Sheaths open, glabrous. Ligules 2–6 mm, acute to acuminate, strongly decurrent, entire, sparsely scabrous abaxially. Panicles narrow, 5–10 cm, spreading at anthesis, branches 2 to 4 per node; spikelets 2- to 5-flowered, 7–10.5 mm, generally at least 4 times as long as wide except at anthesis, more or less terete; glumes somewhat unequal (first 3.8–5.5 × 1.4–1.9 mm, second 4.5–6.7 × 1.8–2.3 mm), acute, 3-nerved, sca-

brous on upper $\frac{1}{3}$ – $\frac{1}{2}$ of keel; lemmas 4.6–6.6 mm, rounded, acute, with erose upper margin, 5-nerved, glabrous to pubescent along lower $\frac{1}{3}$ of keel and marginal nerves, hairs to 0.3 mm; paleas 4–5.8 mm, slightly shorter than lemmas, glabrous; rachilla internodes 0.9–1.9 mm, glabrous; anthers 2.5–4.2 mm, yellow; lodicules 0.6–1.1 mm. Chromosome number $2n = 42$.

DISTRIBUTION. Wenatchee Mountains, central Washington; serpentine soils.

REPRESENTATIVE SPECIMENS. See APPENDIXES 1 and 2.

Poa secunda Presl, Reliq. Haenk. 1: 271. 1830; not Roemer & Schultes, Syst. Veg. 2: 697. 1817, *nomen nudum*. TYPE: ex Cordille[r]ja de "Chili," 1790, *Haenke* (holotype, PR!; isotypes, GH!, MO). FIGURE 24b–m.

Aira brevifolia Pursh, Fl. Amer. Sept. 1: 76. 1814. *Airopsis brevifolia* (Pursh) Roemer & Schultes, Syst. Veg. 2: 578. 1817; not *Poa brevifolia* DC. 1806. TYPE: in the plains of Missouri, *M. Lewis s.n.* (PH). The specimen in the Lewis and Clark herbarium at PH bears the label: "The most common grass through the plains of Columbia R. 10 June 1806." It is probably therefore not the holotype.

Sclerochloa californica Munro ex Bentham, Pl. Hartweg. 342. 1857, *nomen nudum*. *Atropis californica* Munro ex Thurber in S. Watson, Bot. Calif. 2: 309. 1880; *Eragrostis fendleri* Steudel and *Poa andina* Nutt. as synonyms. *Poa californica* (Munro ex Thurber) J. M. Coulter, Manual Bot. Rocky Mtn. Region, 420. 1885; not Steudel, 1854. SYNTYPES: California, San Francisco, *Bolander s.n.*; California, ["in valle Sacramento,"] *Hartweg 2035* (GH!).

Poa tenuifolia Buckley, Proc. Acad. Nat. Sci. Philadelphia, 1862: 96. 1863; not A. Rich. 1851. *Poa buckleyana* Nash, Bull. Torrey Bot. Club 22: 465, *nomen novum*. *Atropis tenuifolia* (Buckley) Thurber in S. Watson, Bot. Calif. 2: 310. 1880. *Panicularia nuttaliana* Kuntze, Rev. Gen. Pl. 2: 783. 1891. TYPE: Columbia R., *Nuttall s.n.* (holotype, PH!; isotypes, GH!, NY!).

Poa tenuifolia Nutt. ex S. Watson in King, Rep. Geol. Expl. 40th Parallel 5: 387. 1871; neither A. Rich. 1851, nor Buckley, 1863. SYNTYPES: Nevada, E. Humboldt Mtns., alt. 8000 ft, Aug. 1868, and Diamond Mtns., alt. 6500 ft, July 1868, *Watson 1318* (GH!, NY!, US!; specimens mounted together, lectotypification not attempted here). Also numbered 1318: Nevada, Virginia Mtns., alt. 6000 ft, Aug. 1867 (GH!, US!); Nevada, Pah-Ute Mtns., alt. 5000 ft, June 1868 (GH!, US!).

Poa tenuifolia Nutt. ex S. Watson var. *elongata* Vasey in Rothrock in Wheeler, Rep. U. S. Geogr. Survey W. 100th Meridian 6: 290. 1878. *Poa buckleyana* Nash var. *elongata* (Vasey) M. E. Jones, Contr. W. Bot. 14: 14. 1912. TYPE: Colorado, Twin Lakes, 1873, *Wolf 1141* (holotype, US!).

Poa tenuifolia Nutt. ex S. Watson var. *rigida* Vasey in Rothrock in Wheeler, Rep. U. S. Geogr. Survey W. 100th Meridian 6: 290. 1878, *nomen nudum*.

Poa andina Nutt. ex S. Watson in King, Rep. Geol. Expl. 40th Parallel 5: 387. 1897; not Trin. 1835–36. TYPE: Colorado, Trinity Mtns., alt. 5000 ft, May 1868, *Watson 1319* (holotype, US!; isotype, NY!). Also numbered 1319: Colorado, E. & W. Humboldt Mtns. (NY!); Nevada, Clover Mtns. (NY!, US!).

Poa andina Nutt. ex S. Watson var. *spicata* Vasey in Rothrock in Wheeler, Rep. U. S. Geogr. Survey W. 100th Meridian 6: 290. 1878. SYNTYPES: Colorado, 1873, *Wolf 1135, 1136, 1137* (US, not seen).

Poa andina Nutt. ex S. Watson var. *major* Vasey in Rothrock in Wheeler, Rep. U. S. Geogr. Survey W. 100th Meridian 6: 290. 1878. SYNTYPES: Arizona, 1872, *Wolf 1133* (US, not seen); Colorado, 1873, *Wolf 1134* (US, not seen).

- Atropis pauciflora* Thurber in S. Watson, Bot. Calif. 2: 310. 1880. *Poa pauciflora* (Thurber) Bentham ex Vasey, Grasses U. S. 42. 1883; not Roemer & Schultes, 1817. *Panicularia thurberiana* Kuntze, Rev. Gen. Pl. 2: 783. 1891, *nomen illegit.* *Poa thurberiana* (Kuntze) Vasey, U. S. D. A. Div. Bot. Bull. 13: pl. 84. 1893, *nomen illegit.* TYPE: California, Sierra Valley, 1871, *Lemmon s.n.* (holotype, NY!).
- Atropis scabrella* Thurber in S. Watson, Bot. Calif. 2: 310. 1880. *Poa scabrella* (Thurber) Bentham ex Vasey, Grasses U. S. 42. 1883. *Panicularia scabrella* (Thurber) Kuntze, Rev. Gen. Pl. 2: 783. 1891. *Puccinellia scabrella* (Thurber) Ponert, Feddes Repert. 84: 740. 1974. TYPE: California, Oakland, *Bolander s.n.* (holotype, NY!).
- Poa nevadensis* Vasey ex Scribner, Bull. Torrey Bot. Club 10: 66. 1883. *Atropis nevadensis* (Vasey ex Scribner) Beal, Grasses N. Amer. 2: 577. 1896. *Puccinellia nevadensis* (Vasey ex Scribner) Ponert, Feddes Repert. 84: 740. 1974. TYPE: S. Utah, N. Arizona, etc., 1877, *Palmer 474* (NY!). The label data on the specimen at NY agree with those originally cited, and this is an isotype. However, the specimen at US, "Austin, Nevada, M. E. Jones 1882," is sometimes cited as the type. It bears the following note signed "AC [Agnes Chase] Aug. 1951": "Specimen in Nat. Herb. named 'Poa nevadensis Vasey' in Vasey script is 'Austin Nevada ME Jones 1882.' Since Vasey is given as author by Scribner his specimen was taken as type by ASH."
- Poa tenuifolia* Nutt. ex S. Watson var. *scabra* Vasey ex Scribner, Bull. Torrey Bot. Club 10: 66. 1883, *nomen nudum.*
- Glyceria canbyi* Scribner, Bull. Torrey Bot. Club 10: 77. figs. 1-4. 1883. *Atropis canbyi* (Scribner) Beal, Grasses N. Amer. 2: 580. 1896. *Poa canbyi* (Scribner) Howell, Fl. NW. Amer. 1: 764. 1903. *Puccinellia canbyi* (Scribner) Ponert, Feddes Repert. 84: 739. 1974. TYPE: Cascade Mtns., Washington Terr., Aug. 1882, *Tweedy & Brandegees s.n.* (holotype, US?, not seen).
- Poa orcuttiana* Vasey, W. Amer. Sci. 3: 165. 1887. TYPE: California, near San Diego, Chollas Valley, 26 May 1884, *Orcutt 1070* (holotype, US!).
- Poa filifolia* Vasey, Contr. U. S. Natl. Herb. 1: 271. 1893. TYPE: Idaho, Nez Perce Co., on rocky banks of Hatwai Creek, 1892, *Sandberg 138* (holotype, US?, not seen; isotypes, GH!, NY!, PH!).
- Poa gracillima* Vasey, Contr. U. S. Natl. Herb. 1: 272. 1893; not Rendle, 1904. *Poa gracillima* Vasey, Grasses U. S. 42. 1883, *nomen nudum.* TYPE: Washington Terr., Mt. Paddo, *Suksdorf s.n.* (holotype, US!; isotypes, NY!, PH!).
- Festuca spaniantha* Philippi, Anal. Univ. Chile 94: 174. 1896. TYPE: *sine loco*, *Anonymous s.n.* (SGO, not seen, *fide* Arnow, Syst. Bot. 6: 418. 1981).
- Festuca patagonica* Philippi, Anal. Univ. Chile 94: 174. 1896. TYPE: [Chile,] ad lacuna Pinto in Patagonia australi, *Ibar s.n.* (SGO, not seen, *fide* Piper, Proc. Biol. Soc. Wash. 18: 147. 1905).
- Poa laevis* Vasey, Contr. U. S. Natl. Herb. 1: 273. 1893; neither Borbás, 1877, nor R. Br. 1810. *Atropis laevis* (Vasey) Beal, Grasses N. Amer. 2: 577. 1896. *Puccinellia laevis* (Vasey) Ponert, Feddes Repert. 84: 739. 1974. TYPE: Montana, North Fork Smith R., 19 July 1883, *Scribner s.n.* (holotype, US!; isotype, NY!).
- Poa laevigata* Scribner, Bull. U. S. Div. Agrost. 5: 31. 1897. *Poa nevadensis* var. *laevigata* (Scribner) M. E. Jones, Contr. W. Bot. 14: 14. 1912. TYPE: Wyoming, Green R., 25 June 1896, *Scribner 2039* (holotype, US?, not seen).
- Atropis laevis* (Vasey) Beal var. *rigida* Beal, Grasses N. Amer. 2: 578. 1896. TYPE: Utah, Lake Point, 19 July 1879, *M. Jones 1021* (holotype, MSC!).
- Poa lucida* Vasey, Contr. U. S. Natl. Herb. 1: 274. 1893. TYPE: Colorado, on mountain sides near Georgetown, [Clear Creek Co.,] 3 July 1885, *Patterson 73* (holotype, US!). At PH are two specimens bearing the same number collected at Georgetown, Colorado, 18 July 1892.
- Poa sandbergii* Vasey, Contr. U. S. Natl. Herb. 1: 276. 1893. *Poa buckleyana* var. *sandbergii* (Vasey) M. E. Jones, Contr. W. Bot. 14: 14. 1912. *Paneion sandbergii*

- (Vasey) Lunell, Amer. Midl. Naturalist **4**: 223. 1915. TYPE: Idaho, near Lewiston, 1892, *Sandberg 164* (holotype, US!; isotypes, GH!, NY!).
- Atropis tenuifolia* (Buckley) Thurber var. *stenophylla* Vasey ex Beal, Grasses N. Amer. **2**: 580. 1896 (as *stenophylla*). *Poa buckleyana* var. *stenophylla* (Vasey) M. E. Jones, Contr. W. Bot. **14**: 14. 1912. TYPE: Oregon, 1887, *Howell s.n.* (not seen).
- Poa capillaris* Scribner, Bull. U. S. Div. Agrost. **11**: 51. fig. 11. 1898; not L. 1753. *Poa nudata* Scribner, Circ. U. S. Div. Agrost. **9**: 1. 1898, *nomen novum*. TYPE: California, Portero, 9 April 1892, *Anonymous s.n.* (holotype, US!).
- Poa juncifolia* Scribner, Bull. U. S. Div. Agrost. **11**: 52. pl. VIII. 1898. *Poa fendleriana* var. *juncifolia* (Scribner) M. E. Jones, Contr. W. Bot. **14**: 14. 1912. TYPE: Wyoming, Sweetwater Co., Black Rock Springs, Point of Rocks, 13 July 1897, *Nelson 3721* (holotype, US!; isotypes, GH!, NY!).
- Poa wyomingensis* Scribner ex Pammel, Proc. Davenport Acad. Nat. Sci. **7**: 242. 1899. TYPE: Wyoming, Sheridan Co., Big Horn, July 1897, *Pammel 192* (holotype, US!).
- Poa saxatilis* Scribner & Williams, Circ. U. S. Div. Agrost. **9**: 1. 1899. *Poa gracillima* Vasey var. *saxatilis* (Scribner & Williams) Hackel, Allg. Bot. Zeitschr. **21**: 79. 1915. TYPE: Washington, Mt. Rainier, on rock cliffs, alt. 7000 ft, Aug. 1895, *Piper 1964* (holotype, US!).
- Poa leckenbyi* Scribner, Circ. U. S. Div. Agrost. **9**: 2. 1899. *Poa nevadensis* Vasey ex Scribner var. *leckenbyi* (Scribner) M. E. Jones, Contr. W. Bot. **14**: 14. 1912. TYPE: Washington, Klickitat Co., Scott, 5 June 1898, *Leckenby s.n.* (holotype, US!).
- Poa acutiglumis* Scribner, Circ. U. S. Div. Agrost. **9**: 4. 1899. TYPE: Oregon, Grave Creek, 21 May 1884, *Howell s.n.* (holotype, US!; isotype, GH!).
- Poa tenerrima* Scribner, Circ. U. S. Div. Agrost. **9**: 4. 1899. TYPE: ex Calif. Acad. Sci. Herb. 26, *sine loco*, *Anonymous s.n.* (holotype, US!).
- Poa limosa* Scribner & Williams, Circ. U. S. Div. Agrost. **9**: 5. 1899. TYPE: California, Mono Lake, 1866, *Bolander s.n.* (holotype, US!).
- Poa invaginata* Scribner & Williams, Circ. U. S. Div. Agrost. **9**: 6. 1899. TYPE: [California,] Sierra Nevada, Summit Camp, 10 July 1870, *Scribner 20* (holotype, US!).
- Poa incurva* Scribner & Williams, Circ. U. S. Div. Agrost. **9**: 6. 1899. TYPE: Washington, Olympic Natl. Park, moraine of Duckaboose Glacier, alt. 7000 ft, Aug. 1895, *Piper 1989* (holotype, US!).
- Poa ampla* Merr. Rhodora **4**: 145. 1902. TYPE: Washington, Steptoe, 3 July 1901, *Vasey 3009* (holotype, US!).
- Poa laeviculmis* Williams, Bot. Gaz. (Crawfordsville) **36**: 55. 1903. TYPE: Washington, Steptoe, 25 June 1900, *Vasey 3026* (holotype, US!; isotype, NY!).
- Poa confusa* Rydb. Bull. Torrey Bot. Club **32**: 607. 1905. TYPE: Wyoming, Albany Co., Medicine Bow Mtns., 28 July 1900, *Nelson 7787* (holotype, NY!; isotype, US!).
- Poa truncata* Rydb. Bull. Torrey Bot. Club **32**: 607. 1905. TYPE: Colorado, Summit Co., Dillon, 26 Aug. 1896, *Clements 373* (holotype, NY!; isotype, GH!).
- Sporobolus bolanderi* Vasey, Bot. Gaz. (Crawfordsville) **11**: 337. 1886; not *Poa bolanderi* Vasey, 1882. TYPE: Oregon, Multnomah Falls, *Bolander s.n.* (holotype, US?, not seen; isotype, GH!).
- Poa multnomae* Piper, Bull. Torrey Bot. Club **32**: 435. 1905. *Poa gracillima* var. *multnomae* (Piper) C. Hitchc. Vasc. Pls. Pacific Northw. **1**: 661. 1969. TYPE: Oregon, Multnomah Falls, 25 June 1904, *Piper 6459* (holotype, US!; isotype, NY!).
- Poa alcea* Piper, Bull. Torrey Bot. Club **32**: 436. 1905. TYPE: Oregon, on Elk Rock near Portland, 3 June 1904, *Piper 6463* (holotype, US!; isotype, NY!).
- Poa brachyglossa* Piper, Proc. Biol. Soc. Wash. **18**: 145. 1905. TYPE: Washington, Douglas Co., alt. 1300 ft, 22 June 1893, *Sandberg & Leiberg 267* (holotype, US!; isotype, NY!).
- Poa helleri* Rydb. Bull. Torrey Bot. Club **36**: 534. 1909. TYPE: Idaho, Nez Perce Co., Lake Waha, alt. 2000–3500 ft, 20 June 1896, *Heller & Heller 3274* (holotype, US!; isotypes, DS!, NY!).

Poa englishii St. John & Hardin, *Mazama* 11: 64. 1929. TYPE: Washington, Whatcom Co., Mt. Baker Natl. Forest, Bagley Lake, 14 Aug. 1928, *Hardin & English 1391* (holotype, WSU!; isotype, US!).

Poa juncifolia Scribner subsp. *porteri* Keck ex Porter, Fl. Wyoming 3: 24. 1964. TYPE: Wyoming, Albany Co., Pole Mtn. region, 6 July 1943, *Porter 3249* (holotype, NY!; isotypes, CI, RM).

Plants caespitose, 1.5–11 dm, sometimes glaucous, frequently becoming red later in season; branching intravaginal; culms 0.3–1.4 mm thick just below inflorescence. Basal leaves 3–80 cm \times 0.4–3(–4) mm, usually much shorter than culms, sometimes so narrow as to appear involute, flat or becoming folded on drying, tip often drying early, scabrous on abaxial midvein and usually on margin (especially near tip), occasionally scabrous throughout. Flag leaves 0.2–22 cm \times 0.4–4 mm, borne near midpoints of culms. Sheaths open, or closed only ca. $\frac{1}{8}$ of length, glabrous or scabrous on margin or throughout. Ligules 0.5–6.5 mm, occasionally obtuse to truncate to more often acuminate, decurrent, entire, becoming erose or lacinate with age, generally sparsely scabrous abaxially. Panicles narrow, 2–27 cm, spreading at anthesis (and remaining open in some plants), the branches 2 to 8 per node, most commonly 3 or 4, some floriferous only near tip, others nearly to base; spikelets 1- to 6-flowered, 3.5–12 mm, generally 4 times as long as wide except at anthesis, more or less terete; glumes somewhat unequal (first 2–5 \times 0.7–1.8 mm, second 2.5–6 \times 1–2.3 mm), acute, more or less erose at margins, 3- (to 5-)nerved, scabrous on upper $\frac{1}{3}$ – $\frac{1}{2}$ of keel, sometimes also scabrous next to keel; lemmas 2.9–6.1 mm, not conspicuously keeled, acute at apex, with erose upper margin, 5-nerved, scabrous throughout, entirely glabrous, or pubescent up to $\frac{2}{3}$ of lower part of lemma, with hairs evenly distributed or extending higher on keel and marginal nerves, to 0.3 mm long, then scabrous above; calluses often with tuft of hairs; paleas 2.5–5.6 mm, equaling or slightly shorter than lemmas, scabrous to pubescent the length of marginal nerves, glabrous to scabrous or pubescent between nerves; rachilla internodes 0.6–1.9 mm, often remaining attached to floret below, glabrous to scabrous or pubescent; anthers 1–3.8 mm, yellow or purple or both; lodicules 0.3–1 mm. Chromosome number $2n = 44, 56, 61–66, 68, 70–72, 78, 81–106$.

DISTRIBUTION AND ECOLOGY. *Poa secunda* is distributed throughout western North America from the Yukon to northern Mexico, and it extends eastward across the northern Great Plains to a few isolated populations north of the Great Lakes and on the Gaspé Peninsula (MAP 1). In addition, there are several disjunct populations in Chile; these are described in detail by Arnow (1981). The Gaspé representatives of *P. secunda* occur in isolated populations on limestone outcrops and seem not to colonize all available habitats. These populations are small (generally fewer than 50 plants), and seed set and plant vigor appear to be low.

The members of the complex grow on a variety of substrates—generally neutral to strongly alkaline soils, which sometimes contain high amounts of soluble salts. Plants with open panicles and short ligules occur only on the walls

of wet, mossy gorges near Multnomah Falls above the Columbia River in Oregon. Those with open panicles but long, acuminate ligules are montane and are found most frequently in crevices in granite. Large, glaucous plants are often found in saline basins, although they are by no means restricted to such areas. The remaining forms in the complex are widespread from sea level to alpine areas up to 4000 m, growing on sites that dry out early in the season. Blooming time is early in the growing season, varying from April to July depending on latitude and altitude.

REPRESENTATIVE SPECIMENS. See APPENDIXES 1 and 2. A full list of specimens examined is on file in the library of the Arnold Arboretum and Gray Herbarium.

NOMINA EXCLUDENDA

These names have been included in the *Poa secunda* complex by some previous workers, but the affinities of the plants to which they refer appear to lie elsewhere for the reasons cited.

Poa cottonii Piper, Proc. Biol. Soc. Wash. **18**: 146. 1905, as *cottoni*. TYPE: Washington, Yakima Co., Rattlesnake Mtns., 7 May 1902, *Cotton 557* (holotype, US!; isotype, NY!). Excluded because the spikelets are large relative to the size of the plant, making it look more similar to *P. cusickii* (for a discussion of which, see introduction).

Poa macroclada Rydb. Bull. Torrey Bot. Club **32**: 604. 1905. TYPE: Colorado, Gunnison Watershed, Roger's, elev. 9000 ft, 14 Aug. 1901, *Baker 802* (holotype, NY!). Excluded because of the small spikelets and the diffuse panicle that suggest affinities with *P. interior*.

Poa fibrata Swallen, J. Wash. Acad. Sci. **30**: 210. 1940. TYPE: California, Siskiyou Co., 3 mi S of Grenada, Shasta Valley, alt. 2600 ft, 30 June 1935, *Wheeler 3629* (holotype, US!; isotype, NY!). Excluded because of extravaginal branching.

Poa napensis Beetle, Leafl. West. Bot. **4**: 289. 1946. TYPE: California, Napa Co., 2 mi N of Calistoga at Myrtle Dale Hot Springs, 7 May 1946, *Beetle 4256* (holotype, UC!; isotype, NY!). Excluded because of the unusually short rachilla internodes and the more nearly ovate glumes.

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APPENDIX 1. **Specimens measured for evaluation of morphological variation using principal-component analyses.**

Canada. YUKON TERRITORY: vic. of Mackintosh (mi 1022, Alaska Hwy.), *Schofield & Crum 7475* (DS); Canol Rd., mi 95, Upper Rose R. valley, elev. 3600 ft, *Porsild & Breitung 10345* (GH). BRITISH COLUMBIA: Allies Mine, Tranquille, 4000 ft, *Dominion Range Exp. Sta. 86* (US); on ridges between Baldy Mtn. and Dunn Peak ca. 7 mi ENE of Littlefort, ca. 51°27'N, 120°03'W, ca. 7000 ft, *Calder, Parmelee, & Taylor 19911B* (DAO); Vancouver Is., Esquimault, *Macoun 71* (US). NORTHWEST TERRITORIES: Mackenzie Distr., N. of Brintnell L. Camp, alt. 3500 ft, *Raup & Soper 9668* (A); Mackenzie Distr., Slave R. lowlands on E side of Slave R., NE Ann's prairie, 60°46'N, 112°44'W, *Reynolds 27* (DAO). ALBERTA: Waterton Lakes Natl. Park, Mt. Crandell, elev. 7500 ft, *Breitung 17405* (US); Webster Twp., Manyberries, *Campbell 85B* (DAO); Beaverlodge, Truax Farm, E of town, *Barkworth 1460* (DAO). MANITOBA: Medora, *Dore 11067* (DAO); Brandon, *Stevenson F121* (DAO). SASKATCHEWAN: Regina, *Shevkenek 15* (DAO); Watman, *Groh s.n.* (DAO). ONTARIO: Flowerpot Is., *Barkworth 2001* (DAO). QUÉBEC: Gaspé Co., stony summit of Mt. Ste. Anne, Percé, *Pease 36592* (GH); Rimouski Co., Pointe aux Corbeaux to Cap Caribou, Bic, *Fernald & Collins 899* (GH).

United States. ALASKA: Juneau, *Hitchcock 4072* (US);* Skagway, *Hitchcock 4206* (US). WASHINGTON: Chelan Co., alpine crest of Three Brothers Peak, 7000 ft, *Thompson 12625*

*Not a member of the *Poa secunda* complex. Eliminated from most analyses.

†*Poa curtifolia*.

(us); † Cowlitz Co., wet cliffs near Smelt Landing, *Thompson 12729* (GH); Kittitas Co., ¼ mi above Teanaway R. (N Fork) on trail to Ingalls Lake, *Kruckeberg 5037* (CAS); † Kittitas Co., Mt. Stuart region, 5000 ft, *Thompson 7813* (US), † *Thompson 7820* (US); † Kittitas Co., open talus slopes at head of Beverly Creek, 5000 ft, *Thompson 9511* (DS); † Kittitas Co., on Beverly Turnpike Trail, Wenatchee Mtns. at 5200 ft, *Kellogg 232** (field- and garden-grown specimens); † Yakima Co., Rattlesnake Mtn., *Cotton 556* (US); Pullman, *Piper 3973D* (US). OREGON: banks of Willamette R., *Howell 33* (US); Gilliam Co., W-facing slope on E side of Phillippi Canyon Rd., 3 mi S off Hwy. 80, and W of Blalock, *Kellogg 22* (field-, greenhouse-, and garden-grown specimens); Grant Co., on steep sandy cut-bank next to rd. along E side of S Fork John Day R., 11 mi S of John Day, *Kellogg 154* (field-, garden-, and greenhouse-grown specimens); Multnomah Co., on Oneonta Gorge Trail not far W of Horsetail Falls, *Kellogg 264*. CALIFORNIA: Tia Juana Valley, *Pringle s.n.*, 6 April 1882 (CAS); El Dorado Co., between Shingle Springs and El Dorado, *Heller 12297* (GH); San Bernardino Co., Mojave Desert, 15 mi NE of Barstow on Garlic Springs Rd., ⅘ mi N of 2nd summit, alt. 2800 ft, *Wolf 6516* (GH); San Bernardino Mtns., flats near Lost Creek, alt. 6800 ft, *Munz 17080* (GH); Siskiyou Co., Yreka, *Butler 1294* (GH); mtns. S Dixey Valley, *Davy s.n.*, 5 July 1894 (US). IDAHO: Clark Co., at U. S. Sheep Exp. Sta. between Spencer and Dubois, E of Rte. 15, 50 yd E of RR tracks, *Kellogg 56* (field- and garden-grown collections; 8 separate culms of field-grown clump scored as separate plants); Elmore Co., 13 mi NE of Mountain Home, on N slopes near headwaters of Rattlesnake Creek, *Christ & Christ 16655* (US); Bitterroot Natl. Forest, Salmon Mtn., *Kellogg 226* (garden- and greenhouse-grown collections); Lemhi Co., on rock outcrop at 9400 ft, 1 mi E of Doublesprings Pass and SW of Buck Creek, *Kellogg 196* (field-, garden-, and greenhouse-grown collections); Lemhi Co., just below microwave relay station near rd. running N from Bannock Pass (3 mi from pass), *Kellogg 221*. NEVADA: vic. of Reno, Hunter Creek Canyon, *Hitchcock 10554* (US); Washoe Co., Dinsmore Camp, Hunter Creek Canyon, 6000 ft, *Kennedy 1639* (CAS). UTAH: slope of Aquarius Plateau, alt. 9000 ft, *Ward 488* (US); SW side of Bald Mtn., elev. 11,500 ft, *Maguire 4004* (US); Cache Co., meadows 3 mi W of Logan, *Maguire 13874* (DAO). ARIZONA: Mojave Co., Mokiak Springs, 19 mi S of Saint George, Utah, alt. 3000 ft, *Gould 1643* (GH); Pipe Spring, alt. 5000 ft, *M. Jones 5266* (DS). MONTANA: Glacier Natl. Park, on large nearly bare rock above McDermott, *Hitchcock 11301* (US); Glacier Natl. Park, Greenwood's Camp, 4500 ft alt., *M. Jones s.n.*, 15 Aug. 1910 (US); Glacier Natl. Park, near E entrance, *Swallen 6458d* (US). WYOMING: Jacksons Hole, above Leighs Lake, alt. 9000 ft, *Merrill & Wilcox 341* (US); Yellowstone Natl. Park, S of Mt. Washburn, *Hitchcock 2036* (US). COLORADO: Gunnison Co., NW Castle Peak, Gothic Basin, ca. 12,000 ft, *Ewan 11752* (US); Rabbit Ear Pass, *Swallen 1379* (US); Moffat Co., W rim of Lodore Canyon, elev. 7500 ft, *Porter 3670* (GH). NEW MEXICO: Fitzgerald Cienaga, *Wootton s.n.* (US). NORTH DAKOTA: Billings Co., edge of Moody Plateau, *Swallen 5787* (DAO); Wells Co., Harvey, *Stevens 1208* (DAO). SOUTH DAKOTA: Black Hills, Custer, *Hitchcock 11107* (US); Pennington Co., near Wall, *Palmer 37278* (GH). NEBRASKA: Chadron, *Bates s.n.* (GH); Dawes Co., *Tolstead 7* (US). MICHIGAN: Isle Royale, Monument Rock, Tobin Harbor, *McFarlin 2175* (US). MINNESOTA: Ottertail Co., Perham, *Chandonnet 2562* (GH). MAINE: North Berwick, *Parlin 1233* (US).

APPENDIX 2. **Specimens measured for discriminant analyses and evaluations of population variation.‡**

United States. CALIFORNIA. San Diego Co.: Cleveland Natl. Forest, T15S R5E, on road from Cibbett's Flat, *Kellogg & Taylor 295* (**1**; 4 sheets); on W side of hwy. N of Mt. Laguna ca. 1 mi, *Kellogg & Taylor 298* (**2**; 4 sheets); N end of Cuyamaca Reservoir, *Kellogg & Taylor 300* (**3**; 3 sheets); on rocky outcrops at N end of Cuyamaca Reservoir, *Kellogg & Taylor 302* (**4**; 3 sheets). Riverside Co.: on N side of Hwy. 74, T7S R4E S16,

*One specimen of each Kellogg collection is at A.

‡Numbers in boldface refer to population numbers on bar graphs.

Kellogg & Taylor 304 (5; 4 sheets); next to Hwy. 79 E of Rancho California (Temecula) on river banks, *Kellogg & Taylor 307* (6; 4 sheets). San Bernardino Co.: on Fort Irwin Rd. ca. 14 mi NE of Barstow, 0.9 mi beyond 2nd summit in side canyon 200 yd from rd., *Kellogg & Taylor 314* (7; 4 sheets). Kern Co.: in Red Rock Canyon, ca. 20 mi N of Mojave on steep slopes W of Hwy. 14, *Kellogg & Taylor 315* (8; 3 sheets). Los Angeles Co.: T7N R16W S13, in canyon ca. 100 yd below Upper Shake Campground, *Kellogg & Taylor 316* (9; 8 sheets); T8N R17W S29, on cut-bank above County rd. N2, *Kellogg & Taylor 321* (10; 4 sheets). Santa Barbara Co.: ca. ¼ mi W of LaCumbre Peak, Santa Ynez Mtns., ca. 3800 ft, *Kellogg & Taylor 322* (11; 3 sheets); on steep N-facing road-cut on N side of Gato Ridge on oil co. property, ca. 900 ft, *Kellogg & Taylor 323* (12; 4 sheets). Mono Co.: just below Carnegie Inst. Transplant Garden, Timberline Exp. Sta., *Kellogg & Kiest 370* (16; 5 sheets); Minarets Wilderness, on River Trail between Garnet Lake and Shadow Lake turnoffs, *Kellogg & Kiest 377* (17; 4 sheets). Inyo Co.: Big Pine Lakes, head of Big Pine Creek between First and Second lakes, elev. 10,000 ft, T9S R32E S33 NW¼, *Kellogg & Kiest 379* (18; 4 sheets). Fresno Co.: just W of Swede Lake, W of Three Sisters, Dinkey Lakes area, ca. 40 mi NE of Fresno, T9S R26E S12 SE¼, *Kellogg & Kiest 382* (19; 4 sheets). WASHINGTON. Ferry Co.: sandy W shore of Columbia R. at Inchelium, below 1290 ft level, *Rogers 531* (20; CAS, DS, GH). Grant Co.: border of alkaline pond in Grand Coulee 7 mi above Dry Falls, *Rogers 589* (21; CAS, DS, GH, US). Kittitas Co.: canyon of Bushy Creek, alt. 1000 ft, *Cotton 1620* (22; GH, US), *1621* (22; US), *1621½* (22; US); Wawawai, on banks of Snake R., *Piper 2567* (23; GH, US—2 sheets); Coulee City, *Piper 3912—2 sheets, 3916, 3918, 3920—2 sheets* (24; GH, US). Whitman Co.: Albion, 8 mi NW of Pullman in RR right-of-way, *Keck & Hiesey 5340, 5341, 5342* (25; DS). Chelan Co.: alpine slopes of Chumstick Lookout, 6000 ft, *Thompson 14979* (26; CAS, DS, GH). Kittitas Co.: open alpine ridges at head of Beverly Creek, 5000 ft, *Thompson 9511* (27; CAS, DS, GH, US—2 sheets); on Teanaway Divide, Beverly Turnpike Trail, 5700 ft, *Kellogg 233* (28; 5 sheets).

Canada. QUÉBEC. Rimouski Co.: on shale outcrop below calcareous cliffs above St. Fabien sur Mer, *Kellogg & Kiest 351* (13; 8 sheets). Gaspé Co.: Grand Coupe ca. 1 mi NW of Percé, ca. 550 ft alt., *Kellogg & Kiest 358* (14; 7 sheets). Bonaventure Co.: on S-facing cliffs just below summit of Mt. St. Joseph, *Kellogg & Kiest 363* (15; 3 sheets).

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